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A UNIQUE BALANCED BREEDING SYSTEM IN THE VERNAL POOL MOUSE-TAILS[1]

DONALD E. STONE

Tulane University, New Orleans

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As a force in determining the rate of evolution, recombination is given a lead role (Anderson, 1949; Stebbins, 1950; Anderson and Stebbins, 1954). Because of the importance of recombination we are intensely interested in factors which modify and mold new channels of recombination systems. The following study in the mouse-tail genus, *Myosurus,* is focused on a type of recombination system that restricts outcrossing and favors inbreeding through a peculiar type of floral mechanism. It will be shown how a balanced system favoring inbreeding can operate in producing a multitude of biotypes, all of which can exist essentially autonomously and sympatrically. Emphasis is placed on the suitability of such a balanced breeding system in meeting the demands of stringent, fluctuating, environmental conditions.

Accumulated evidence suggests that peculiar mechanisms affecting the breeding systems of plants and animals are not merely happen-chance occurrences, but rather they are timely adaptations which harmonize with pressures of natural selection (see Baker, 1953; Stebbins, 1957). In certain genera of grasses the breeding systems have been shown to be distributed not at random, but in fact they are rather closely correlated with a number of other characters, as for example the annual plant habit and self-pollination (Stebbins, 1950). Experimental evidence suggesting the selection of breeding systems per se comes from such work as that on *Primula vulgaris* (Crosby, 1949). In certain populations the appearance of a homostyle condition was shown to increase in numbers at the expense of the pins and thrums, in spite of sporophytic superiority of the latter. Selection for the gametically superior homostyle-type was only partially offset by the contra-selection of its inferior sporophyte. Thus natural selection acting upon the hereditary components of the plants or animals elicits specific responses that bring the sum total of the individual's life cycle in tune with their surroundings.

While "progressive evolution" as formulated by Wright (1931, 1956) is realized only in the exclusive outcrossing

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system, adaptation to the myriad of ecological niches has revolved in some cases around a balance between outcrossing and inbreeding. In hermaphroditic animals and monoecious plants, between the extremes of outcrossing and inbreeding, there lies an array of breeding types which are the result of a compromise between fitness—normally secured through homozygosity—and flexibility—secured through heterozygosity. This balance has been termed the "hybridity equilibrium" by Darlington and Mather (1952).

Proceeding from the fact that homozygous individuals are well suited for prescribed conditions, i.e. they have a high degree of fitness, Stebbins (1950) has postulated that those individuals which would be most in need of a self-fertilization system are ones that are subjected not only to extreme conditions such as deserts, alpine or arctic regions, but also

FIG. 1. Map of Great Valley of California, with the location of a few *Myosurus* populations studied in detail.

to environments which have great climatic fluctuations from year to year. The advantages of self-fertilizing races in extreme fluctuating environments are manifest in the plant's ability to produce large quantities of seed that can tide the race over unfavorable years. The model for a predominant uniparental system of reproduction with occasional lapses into outcrossing pictures each self-fertilizing line or biotype maintaining itself for hundreds of generations until a chance cross-fertilization takes place. Following each chance hybridization there will be a burst of evolution for six to eight generations, during which time segregation and natural selection will act. Certain biotypes will either be eliminated entirely or move on to new ecological niches, while other lines will be better suited to the environment occupied by the parental biotypes. The surviving biotypes will approach homozygosity through continued inbreeding while awaiting new chances for hybridization and population differentiation.

California Central Valley populations of *Myosurus* present just such a problem. They are subjected to the fluctuating environments of vernal pools and hence to the continual shift in the goal of mass selection. Response to these unstable conditions has led to multi-modal patterns of adaptation with the production of numerous biotypes, each offering certain selective advantages and adaptive traits.

Habitat and Ecology of Selected Populations

The populations presented here are samplings from known areas of mouse-tail diversity (see fig. 1 and table 1). Of particular interest is the coincidence of these centers of diversity with the well defined vernal pools that are so characteristic of the Great Valley of California.

Vernal pools or hog-wallows (see figs. 2a, 2b) as defined by Hoover (1937) are "small depressions on the plains in which the soil is a heavy clay, probably underlain at no great depth by hard pan, where water collects in pools during the rainy season." These pools which are formed in the winter months usually overflow with heavy rains, but as the precipitation lessens and evaporation increases, progressively shallower pools are formed until complete dryness takes over in late April or early May and lasts until the first rains in September. Generally the areas where pools occur are poorly defined geographically, though the east (from Butte County to Tulare County) and west (from Glenn County to Merced County) sides of the Great Valley have the clearest examples. Occasionally, however, hog-wallows are found scattered from Shasta County in the north to Kern County in the south.

The factors which govern vernal-pool formation seem to be fairly uniform throughout the valley. In regard to climate, differences within the valley are not as striking as differences between the valley and the Coast and Sierra Nevada Ranges which delimit it. While the wide latitude of temperature, 13° to 118° F., is common throughout the valley, there are north-south and east-west rainfall gradients which undoubtedly influence various aspects of the formation.

Of the many factors which may be collectively responsible for vernal pools, low precipitation, poor drainage, and high evaporation are equally responsible for the genesis of alkali soils. Thus in all populations for which the soil conditions were verified, there existed a close correlation with alkali formations (table 1). It should be noted, however, that the correlation between alkali soils and populations of *Myosurus* may not be directly related through any cause and effect of alkali salts per se, but rather the association may actually be due to a coincidence of alkali salts and other aspects of vernal pools which operate in mouse-tail selection.

The combination of vernal pools and alkali soils presents unique ecological niches which pose a variety of problems for plant survival. In addition to the cyclic water conditions, such pools have

FIG. 2. Population sites of some California mouse-tails. (a) Mapes Ranch (near Modesto), Stanislaus Co., *Myosurus* and salt grass do nicely in this well-defined vernal pool. (b) Hatch Ranch (near Modesto), Stanislaus Co., *Myosurus, Downingia,* and *Navarettia* surrounded by the yellow composite, *Baeria,* in a series of pronounced depressions.

TABLE 1. *California Valley collections, seed sources in progeny tests*

Population & Taxon.	Collection No.	Location	Soil conditions
(1) Willows *M. m. filiformis*	Stone #9	Glenn Co., Ajax Field in city of Willows	———
(2) Maxwell *M. m. filiformis* *M. m. apus* *M. s. alopecuroides* *M. sessilis*	Mason #14508, #14509, #14510; Stone #1, #2, #7, #13.	Colusa Co., 3 mi. e. of Maxwell on Maxwell Rd.	Willows clay, moderate alkali.
(3) Manning Flat *M. minimus*[1] *M. minimus*[2]	Mason #14503, #14504, #14505; Stone #3, #4, #5, #6, #12.	Lake Co., 5½ mi. w. of Lower Lake on the Kelseyville Rd.	Klamath silty clay loam, no report on alkali.
(4) Byron *M. m. filiformis* *M. minimus*[1] *M. minimus*[2] *M. m. apus*[1] *M. m. apus*[2] *M. m. apus*[3] *M. s. alopecuroides* *M. sessilis*[1] *M. sessilis*[2]	Mason #14262, #14263, #14264, #14268, #14269, #14270, #14272, #14273; Stone #8, #14.	Contra Costa Co., 3 mi. s. of Byron on road to Herdlyn.	Solano silty clay, moderate to high alkali.
(5) Crows Landing #1 *M. m. filiformis* *M. minimus*[1] *M. minimus*[2] *M. m. apus*	Mason #14274, #14275.	Stanislaus Co., 5 mi. n.e. of Crows Landing on Crows Landing Rd.	Waukena fine sandy loam, slight to moderate black alkali.
(6) Crows Landing #2 *M. m. filiformis* *M. minimus*[1] *M. minimus*[2] *M. m. apus*	Mason #14288, #14289, #14294, #14295, #14290.	Stanislaus Co., 6 mi. n.e. of Crows Landing at intersection of Hilmar and Morgan Rds.	Waukena fine sandy loam, slight to moderate black alkali.
(7) Hanford *M. m. filiformis* *M. minimus*[1] *M. minimus*[2]	Mason #14501.	Kings Co., 3 mi. e. of Hanford on road to Visalia.	Traver fine sandy loam, high alkali.
(8) Kerman *M. minimus*	Mason #14502.	Fresno Co., 5 mi. s. of Kerman on Madera Ave.	Fresno sandy loam, alkali.
(9) Bakersfield *M. minimus* *M. m. apus*	Stone #11.	Kern Co., n.e. of Bakersfield on highway #178.	———

salt gradients which may result in characteristic local patterns. It is known, for example, that differential diffusion will carry soluble salts up the sides of the pools during the drying-up process and then deposit these salts in bands or rings at various levels in the depression, much like differential diffusion in paper chromatography (Arkley, R. and G. Smith, personal communication). The height of the water table is a factor controlling the widths of the salt bands, due to the fact that capillary action operates only within certain limits. A high water table, in

addition to producing wide salt bands, usually results in higher concentrations of salts in the upper edges of the depression, while the lower basin may be leached relatively free of accumulated salt. Bands with different salts and different concentrations of the same salt can in their selective pattern result in strikingly colorful concentric rings of distinct species of plants.

Secondary effects commonly associated with a high exchangeable Na^{+} of alkali soils, which apparently replaces the critical Ca^{++} constituent, include poor soil aeration due to reduced flocculation of soil particles (Kelley, 1951), high pH, increased osmotic value in the soil solution, and also perhaps reduced bacterial action (Harris, 1920). The sum total of these variables offers a wide variety of ecological niches, but also expresses exacting requirements for survivors. Plants responding to such conditions must have fitness as well as flexibility.

Mechanisms Affecting Isolation and Gene Exchange

The very fact that several—as many as nine biotypes at Byron—morphologically-distinct biotypes occur sympatrically suggests the effective operation of one or more barriers to outcrossing. Early work on single flower isolations showed that self-fertilization was quite effective in initiating normal seed set, while emasculated flowers failed to set any seed. Clues to the type of mechanism responsible for reduced outbreeding were self-evident in the development of the flower; however, little importance was attached to these clues until a number of artificial hybrid combinations between even some of the most extreme species revealed a maximum of 5% pollen abortion and the production of a normal amount of viable seed.

Breeding mechanism. The role of the flower in affecting isolation has of recent been given strong support (Grant, 1949). As recognized by Grant, floral isolation may be affected by structural contrivances of the flowers (mechanical isolation: Dunn, 1956) or by the specificity of certain animal pollinators (ethological isolation: Grant, 1949, 1952; Straw, 1955).

Owing to the peculiar floral development in the mouse-tails, mechanical isolation insuring self-pollination is inherent while limited opportunities also exist for outcrossing. *Myosurus* flowers which are borne singly on scapes (peduncles) have their origin in the basal rosette of linear leaves (Mason, 1957). The solitary green flowers usually have five petaloid sepals; three petals, each of which bear a nectariferous pit at the summit of the slender claw; an average of seven appressed stamens; numerous pistils (10–400) spirally arranged on an elongate receptacle; and after fertilization, numerous achenes with a persistent style (figs. 3a–3d). At the time of meiosis and pollen grain formation the flower buds are buried deep in the leaves and well protected by the enfolding sepals (Stone, 1957). In some biotypes, e.g. *M. sessilis* Wats. and *M. minimus* subsp. *apus* (Greene) Campbell, the buds remain buried in the leaves throughout flowering and maturation, while the long peduncled forms like *M. minimus* var. *filiformis* Greene have an inch or two of peduncle elongation before pollen release and the subsequent elongation during the maturation process.

While several variations in flowering exist, only the patterns displayed by two extreme sympatric morphological types, *M. sessilis* and *M. m. filiformis,* will be discussed. At the time of anther dehiscence in *M. sessilis* the sepals and stamens are about equal in length to the pistil-bearing receptacle. Thus all of the pistils will be pollinated, but as there is a period of several days (3–10 days) before the pistils become receptive immediate fertilization is not affected. In the period following pollen release the sepals in *M. sessilis*—as well as in *M. m. apus*—reflex until the entire receptacle is exposed (fig. 3b). In contrast to flower development in the short-peduncled types, *M. m. filiformis* does not expose the entire receptacle to self-pollination. Rather,

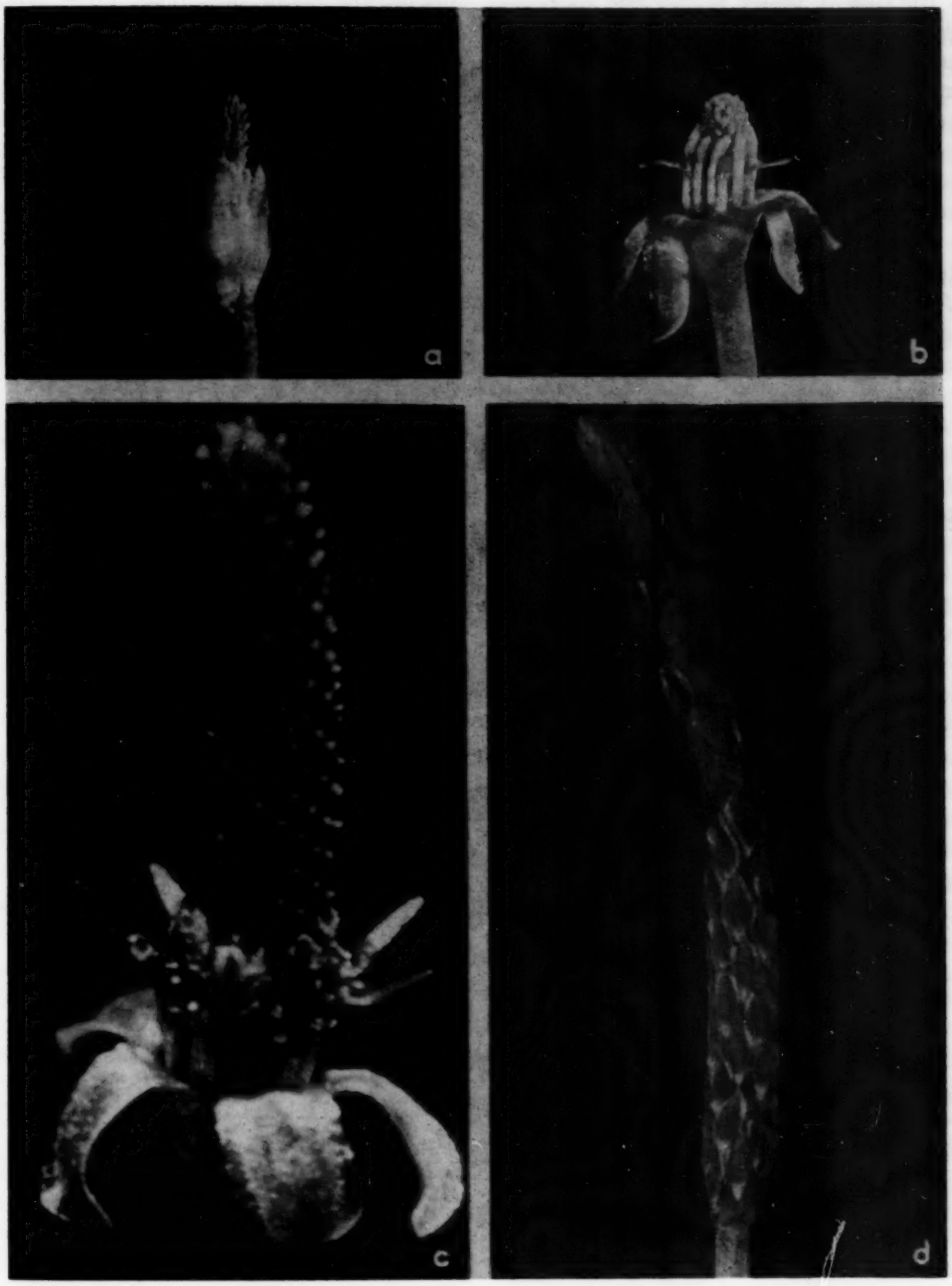

FIG. 3. Stages of flowering in the mouse-tails. (a) Receptacle pushing through closed sepals subsequent to pollination. *M. m. apus* (14269–7#3), × 5. (b) Sepal reflexing normally occurs shortly after pollination, note appressed stamens and two divergent petal blades, *M. m. apus* (14269–7#3), × 5. (c) Continued elongation of the receptable after pollination, note the released pollen grains and exuded nectar drop in the pit of the petal, *M. m. apus* (14269#X), × 10. (d) Normal greenhouse-grown receptacle showing scattered seed set on the upper half, *M. minimus* (14–8#X), × 5.

at the time of pollen release the appressed sepals and stamens are only about one-half as long as the receptacle. Thus pollination will only be affected on the lower half of the receptacle, while the upper portion protrudes above the sepal enclosure, free and clear of the released pollen (see fig. 3d).

It is suggested that self-pollination is almost perfected in *M. sessilis,* while in *M. m. filiformis* inbred seed is predominantly a function of the lower half of the receptacle. The upper half or the receptacle is considered advantageous to cross-fertilization, not only because it has not been pollinated, but also due to the fact that flowers of the *M. m. filiformis* type are borne on elongate scapes which offer good exposure. If it were not for an additional piece of information, the conclusion would be drawn that outcrossing from one flower to the next would almost always be between individuals which have long peduncles and a flower like *M. m. filiformis.* However, examination of flower buds from the time of pollen release to achene maturity has revealed an increase in the number of pistils in *M. sessilis,* but not in *M. m. filiformis* (fig. 4). This evidence suggests that new pistils are being developed after pollen release at the tip of *M. sessilis* flower, probably in response to favorable growing conditions. The effect of this mechanism lies within its ability to further outcrossing by offering unexposed pistils of the *M. sessilis* biotype to foreign pollen.

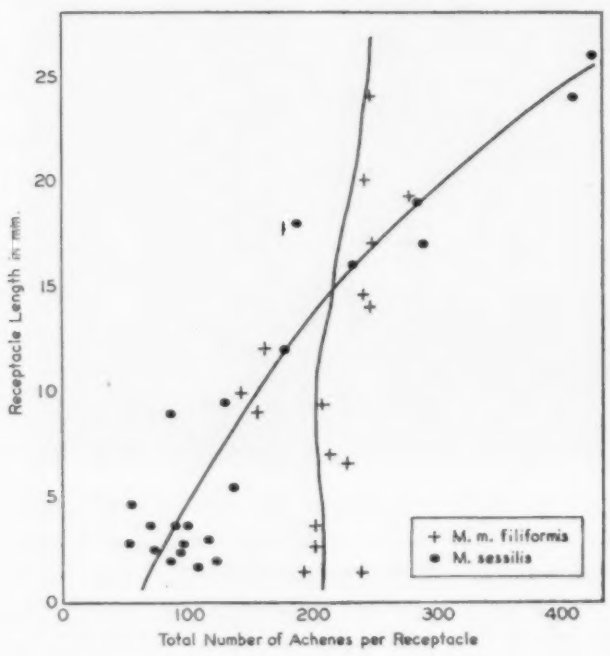

FIG. 4. Receptacle elongation and increase in total number of achenes, from anthesis to maturity, *M. m. filiformis* and *M. sessilis.*

The mechanics of the flower, while insuring inbred seed, offer only limited possibilities for outcrossing. From evidence of natural hybrids collected in the field and tested in the greenhouse, the frequency of outcrossing (between different biotypes at least) is extremely low (Maxwell, 1953, 2% of studied sample). This apparent effective operation of a single isolation mechanism was not given full credit until several other obvious factors were considered: namely, ethological, ecological and seasonal isolation.

Insect specificity. Insect visits probably play a very minor role in the pollination of mouse-tail flowers. Owing to the difficulty of making field observation at appropriate times, evidence against ethological isolation is limited to greenhouse studies and data from investigation on the European *M. minimus* L. (Muller, 1883; Knuth, 1908). Greenhouse material reveals that seed set on the lower half of the receptacle is part of the normal flower development in the absence of insect visitors (see fig. 3d). Observations on European *M. minimus* detected eleven species of insects which infrequently visited flowers, and of these eleven all are classified as promiscuous and relatively unspecialized as pollinators (Knuth, 1906).

Ecological differences. Tolerances and preferences of the mouse-tail biotypes are little understood, especially those which function as microenvironments within a population. However, as it is not uncommon to find extreme biotypes, e.g. *M. sessilis* and *M. m. filiformis* (see figs. 7a and 7d), growing on the same clod of ground, it would seem that ecological conditions are more important in initiating and maintaining autonomous population differentiation. The selective influence of

local conditions is substantiated by biotype variation from population to population.

Seasonal isolation. As evidenced by an out-of-phase flowering pattern, seasonal isolation is only partially realized. Using the extreme sympatric biotypes (*M. sessilis* and *M. m. filiformis*) for comparison, mass plantings of each of these species were made. Germination under the standardized conditions occurred in about 13 days for both groups, this being the median time for all but one of the species investigated. In order to test the rate of flowering, 25 individually potted seedlings of both biotypes were placed side by side in a pan of water. Two details were checked during the growth of each of the plants: the time from planting to the appearance of the first bud; and the time from planting to the first opening flower. Almost without variation the *M. sessilis* plants produced the first visible flower bud about two weeks earlier than *M. m. filiformis* (53 days versus 69 days). The most startling difference, however, was in the fact that flower opening and pollen dehiscence took place around four weeks earlier in *M. sessilis* (61 days versus 86 days). Apparently the elongation of the peduncle in *M. m. filiformis* (see fig. 7d), before flower opening takes place, requires this extra period. Of interest along these lines it can be pointed out that a third row of 25 pots, containing F_2 hybrids between *M. sessilis* × *M. m. filiformis*, had a mean first-bud appearance of 61 days, exactly intermediate between the two parental types.

The continued production of flowers in the greenhouse material completely breaks down the isolation due to flowering time. Field plants, however, frequently do not produce more than one or two flowers and thus would have little if any overlap in flowering. It might well be expected that growing years which favor the production of numerous flowers and flowering overlap also favor hybridization.

Population Structure

The net effect of the balanced breeding mechanism in *Myosurus* is particularly striking in two selected populations from the lower Sacramento Valley area (fig. 1). In the Maxwell population four sympatric biotypes occur, while at Byron nine true-breeding entities were collected. From each of the populations large numbers of samples were taken and individual progeny tested for evidence of heterozygosity. With little difficulty most individuals could be morphologically recognized and conveniently grouped into a number of essentially homozygous biotypes. Evidence from the correlation of a number of characters from both field and greenhouse-grown individuals, in addition to artificial hybridizations, has suggested that the intermediate biotypes occurring in these populations are the result of hybridization and subsequent stabilization through repeated inbreeding.

Diagnostic characters and techniques in analysis. Because of the "streamlined" appearance of the mouse-tails (see figs. 5a–5g) the selection of characters for population studies was necessarily limited to a single vegetative comparison (ratio of the leaf length to the total length of the scape-plus-receptacle, hereafter referred to as the leaf/recepto-scape ratio), and six or so features related to flowering.

The leaf/recepto-scape ratio is in reality an expression of the genetically and phenotypically-variable scape length. Scape length is a multifactorial character that has obvious diagnostic significance; however, it also happens to be subject to a great deal of phenotypic plasticity, affected especially by crowded conditions and water availability. Seldom-watered seedlings were known to have flowered with a scape of less than one-half inch, while sister seedlings growing in saturated soil had scapes up to ten times as long. While the genetic significance of this ratio is reduced because of environmental modification, in general, three distinct classes can be recognized: leaves 2–4 ×

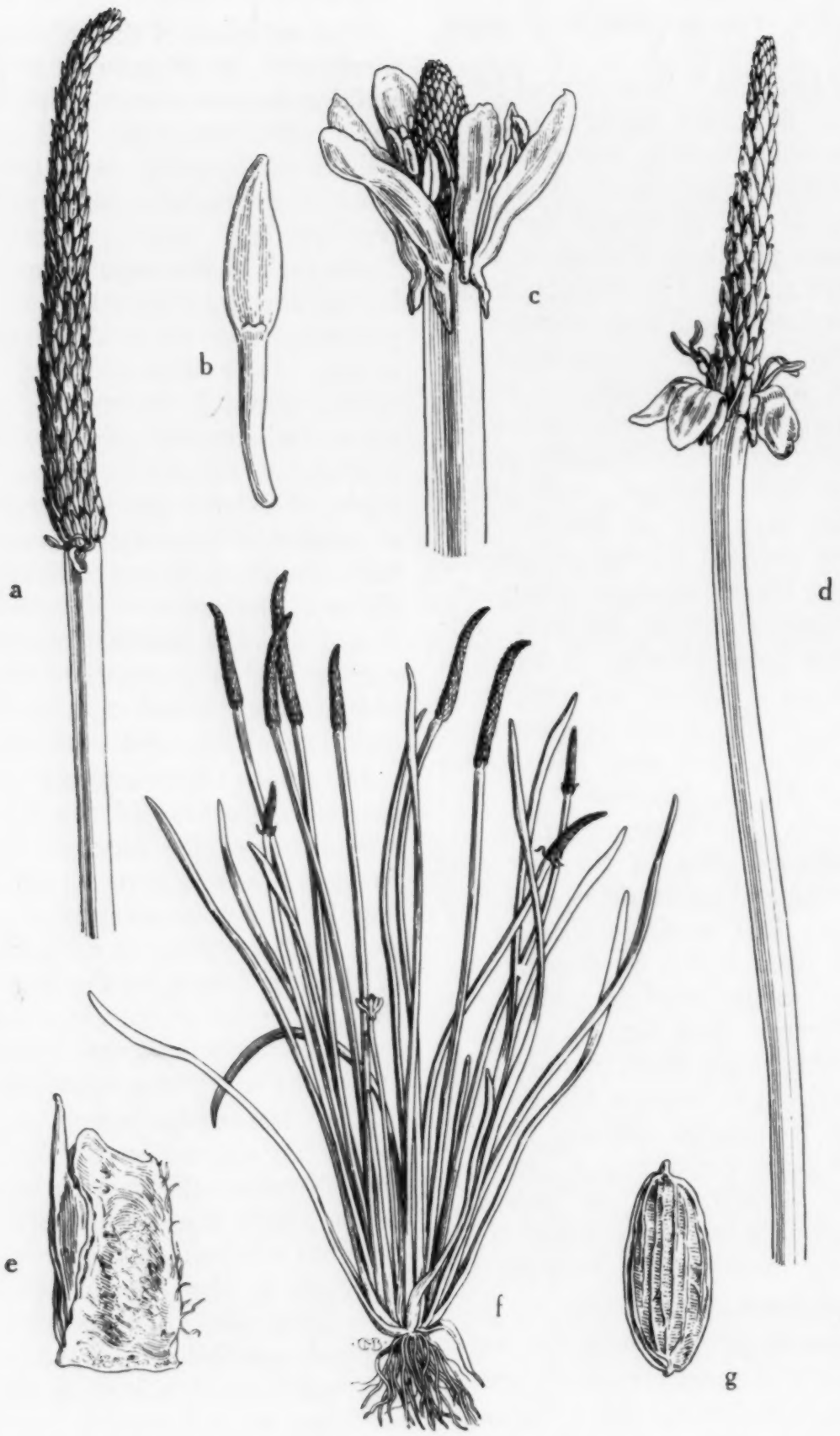

FIG. 5. Plant and flower parts of *M. minimus* (Byron Population) by Mrs. Mary Barnas Pomeroy. (a) Mature fruiting spike, × 2. (b) Petal and terete claw, showing nectariferous pit, × 19. (c) Flower prior to anthesis, with the spurs of the sepals extending below the sepal attachment point, × 5. (d) Young fruiting spike after pollination, × 4. (e) Mature achene from receptacle, note erect beak, × 15. (f) Habit, showing the slender, clavate scapes and the linear, spatulate leaves, × ½. (g) Mature seed, × 18.

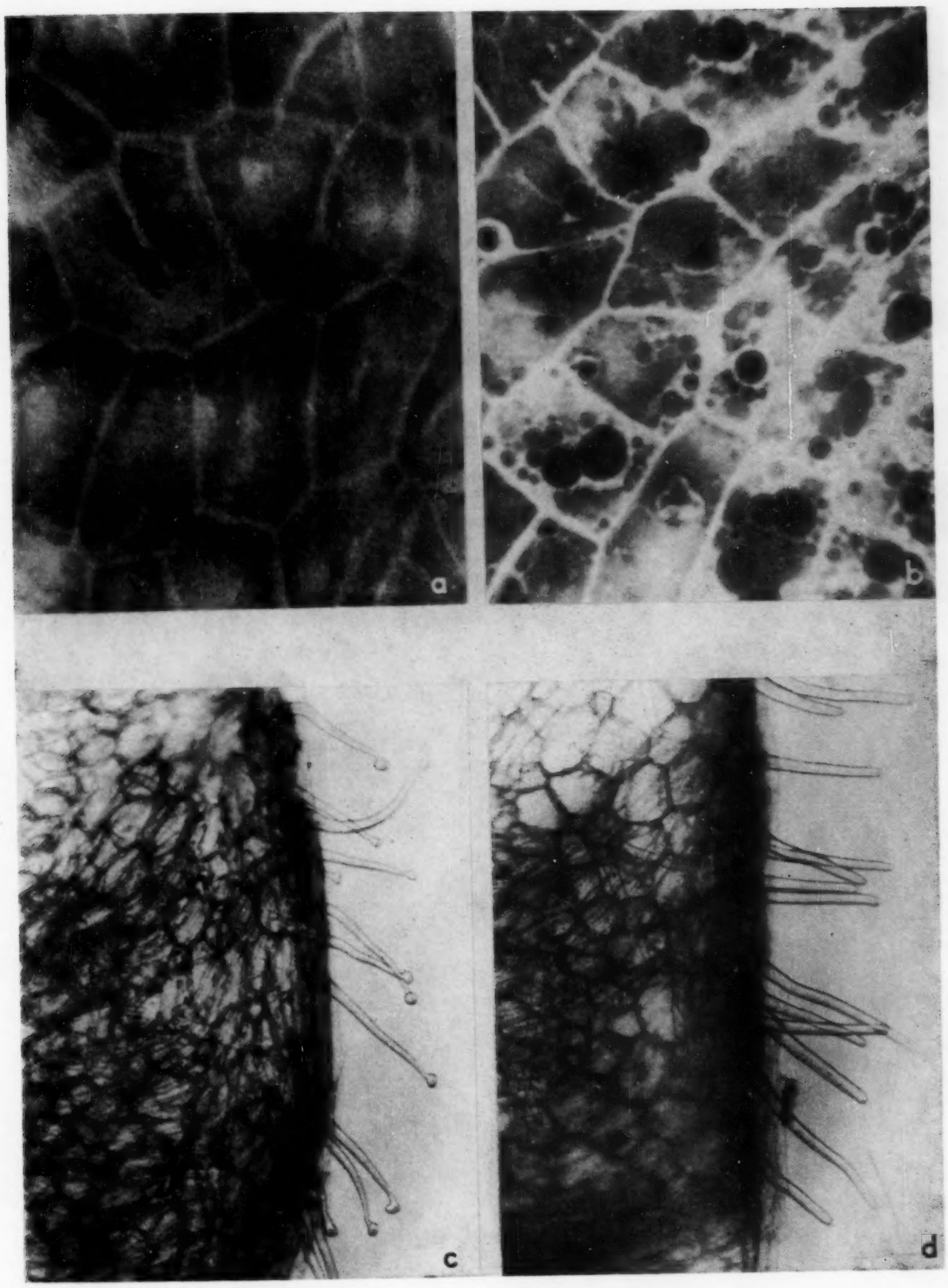

FIG. 6. Seed-coat and achene-hair types. (a) Normal seed, cellular inner integument with dispersed brown pigment, *M. sessilis* (1–1#5), × 675. (b) Speckled seed, cellular inner integument with concentrated brown pigment, *M. sessilis* (8–26#X), × 675. (c) Normal capitate hairs on adaxial side of achene, *M. minimus* (14269#3), × 1000. (d) Non-capitate hairs on adaxial side of achene, *M. minimus* (14268#1), × 1000.

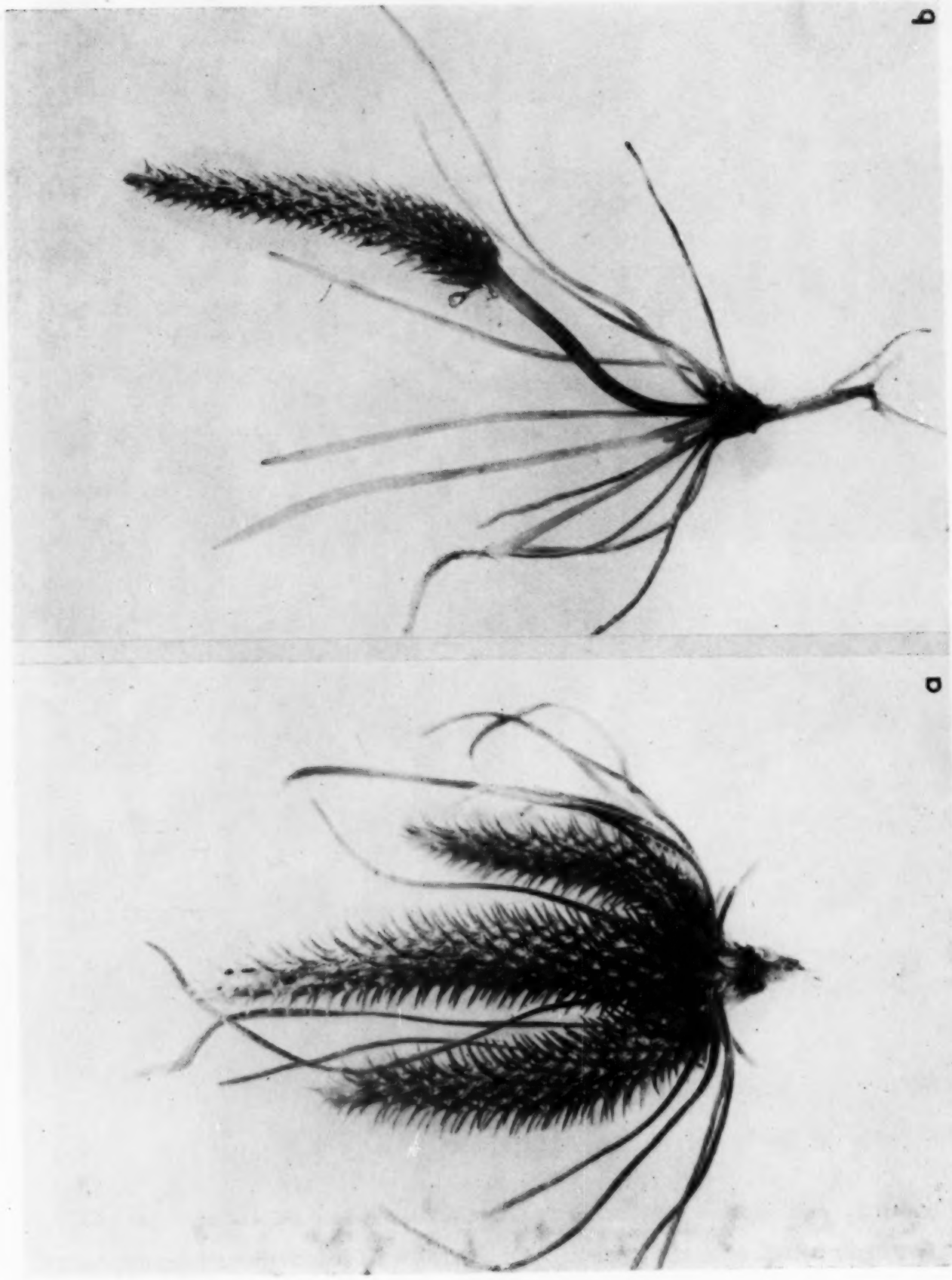

FIG. 7. Biotypes of the Maxwell Population. (a) Leaf/recepto-scape ratio 2–4 ×, *M. sessilis* (14508#7), × 3. (b) Leaf/recepto-scape ratio 1 ×, *M. s. alopecuroides* (14510#14), × 3.

FIG. 7. Biotypes of the Maxwell Population. (c) Leaf/recepto-scape ratio 1 ×, *M. m. apus* (14510#15), × 3. (d) Leaf/recepto-scape ratio ⅔ ×, *M. m. filiformis* (14509#3), × 3.

recepto-scape, *M. sessilis* Wats. (fig. 7a); leaves 1–2 × recepto-scape, *M. sessilis* subsp. *alopecuroides* (Greene) Stone (fig. 7b), and *M. minimus* subsp. *apus* (Greene) Campbell (fig. 7c); and leaves ⅓–½ × recepto-scape, *M. minimus* var. *filiformis* Greene (fig. 7d).

The flower parts and mature achenes provide the best characters for identification. Hereditary differences between length of the sepal spurs (see fig. 5c), for example, were found to be best expressed in a ratio with the blade of the sepal. Certain characters were not readily quantified (e.g. receptacle tapering) while other features of the mature flower were ideal for a quantitative analysis (see figs. 5a–5g). Achenes studied from soaked material (at 30 × or 60 × examination and with a mounted ocular micrometer) were measured for achene length, achene width, stylar-beak length, beak angle, the length and width of the seeds, and pericarp hairs (measurements here being made at 150 ×).

The lack of discrimination between biotypes on the basis of seed size rendered this character useless, however, as a result of this study an unusual speckle-seeded biotype (see figs. 6a–6b) was turned up in the Byron population. A second qualitative feature occasionally encountered in biotypes of the *M. minimus* complex (see fig. 13) is the possession of non-capitate hairs (see figs. 6c–6d). The presence or absence of these two qualitative features has been most useful in delimiting certain difficult biotypes.

Population analyses. The *Maxwell population* has been emphasized mainly because the vernal pool is small (40–50 ft. in diameter), well defined, and has but four morphologically-distinct biotypes that only occasionally are joined by hybrid survivors. The pool which is on the west side of the Sacramento River has a moderately alkaline soil that supports a lush vernal-pool flora; this includes such plants as *Downingia, Plantago, Lepidium,* in addition to the four biotypes of *Myosurus: M. sessilis, M. s. alopecuroides, M. m. apus,* and *M. m. filiformis* (figs. 7a–7d).

The analysis of field-collected individuals and a comparative evaluation of greenhouse-grown progeny revealed a high degree of genetic homogeneity within biotypes (table 2), although certain characters which were readily modified by slight changes in the environment often gave confounding results. Studies of achene variation on a single individual, on selfed progeny grown under varied conditions, and interbiotype comparisons of greenhouse material helped differentiate between genetic modifications and phenotypic plasticity.

The general appearance of the Maxwell biotypes is such that even without detailed studies, a morphological sequence from *M. sessilis* to *M. m. filiformis* can readily be constructed (figs. 8a–8d). Gross characters such as the leaf/recepto-scape ratio, beak angle, and achene size justify the placement of the biotypes in a linear sequence with step-like discontinuities. With but two exceptions, namely the blade/spur ratio and pericarp hair length, all of the quantified characters (table 2) follow an ascending or descending order of arrangement from *M. sessilis,* to *M. s. alopecuroides,* to *M. m. apus,* and then to *M. m. filiformis.* In respect to the blade/spur ratio and the hair length, both characters agree that the position of the two intermediate biotypes is reversed; thus, *M. m. apus* is closer to *M. sessilis* than is *M. s. alopecuroides* on the basis of these two characters.

Hybridization. A random assortment of 25 individuals from each of the four biotypes reveals striking uniformity within biotypes and very discrete differences between them (fig. 9). In contrast to the uniformity displayed by most, four natural-occurring individuals showed extreme segregation for such characters as beak angle, beak length, achene width, etc. These natural hybrids had intermediate morphological characters which placed them either in the *M. s. alopecuroides* or *M. m. apus* group. The occur-

TABLE 2. *Maxwell intra-population statistics*

	sessilis	*alopecuroides*	*apus*	*filiformis*
Leaf/R-Scape	2–4x	1–2x	1–2x	1/2–2/3x
Beak Angle	45–90°	30–45°	0°	0°
Achene length*				
Field:				
$\bar{x} \pm s_{\bar{x}}$	59.1 ± .63	55.9 ± .56	53.7 ± .56	42.5 ± .79
Range	50–74	50–62	46–66	30–53
# indiv.	75	24	27	53
Grnhse.:				
$\bar{x}$	69.9	59.4	58.1	49.8
Achene width*				
Field:				
$\bar{x} \pm s_{\bar{x}}$	49.3 ± .31	32.0 ± .53	26.6 ± .44	21.7 ± .38
Range	38–64	26–36	23–31	17–28
# indiv.	75	24	27	53
Grnhse.:				
$\bar{x}$	44.8	29.7	24.7	24.5
Beak length*				
Field:				
$\bar{x} \pm s_{\bar{x}}$	46.7 ± .54	20.4 ± .33	14.1 ± .43	6.3 ± .23
Range	32–56	16–22	11–17	2–9
# indiv.	75	24	27	53
Grnhse.:				
$\bar{x}$	37.8	16.2	10.6	5.8
Hair length**				
Field:				
$\bar{x}$	29.0	19.2	26.0	12.9
Range	24–33	16–25	20–34	10–20
# indiv.	10	9	13	13
Grnhse.:				
$\bar{x}$	28.9	18.4	23.7	11.2
Blade/Spur				
Grnhse.:				
$\bar{x}$	4.6	3.7	4.4	2.6
Range	3.5–7.2	2.7–4.6	3.7–5.2	2.2–2.9
A.L./B.L.				
Field	1.26	2.73	3.72	6.75
Grnhse.	1.84	3.67	5.50	8.59
A.W./B.L.				
Field	1.05	1.26	1.83	3.43
Grnhse.	1.18	1.83	2.33	4.22

* 40 units = 1 mm.
** 104 units = 1 mm.

rence of these four hybrids is considered as conclusive proof of natural hybridization but also suggests the initiation of intermediate biotypes (i.e. *M. s. alopecuroides* and *M. m. apus*) through hybridization of the extremes (i.e. *M. sessilis* and *M. m. filiformis*).

Confirmation of the role of natural hybridization in synthesizing intermediate groups was partially verified by reciprocal

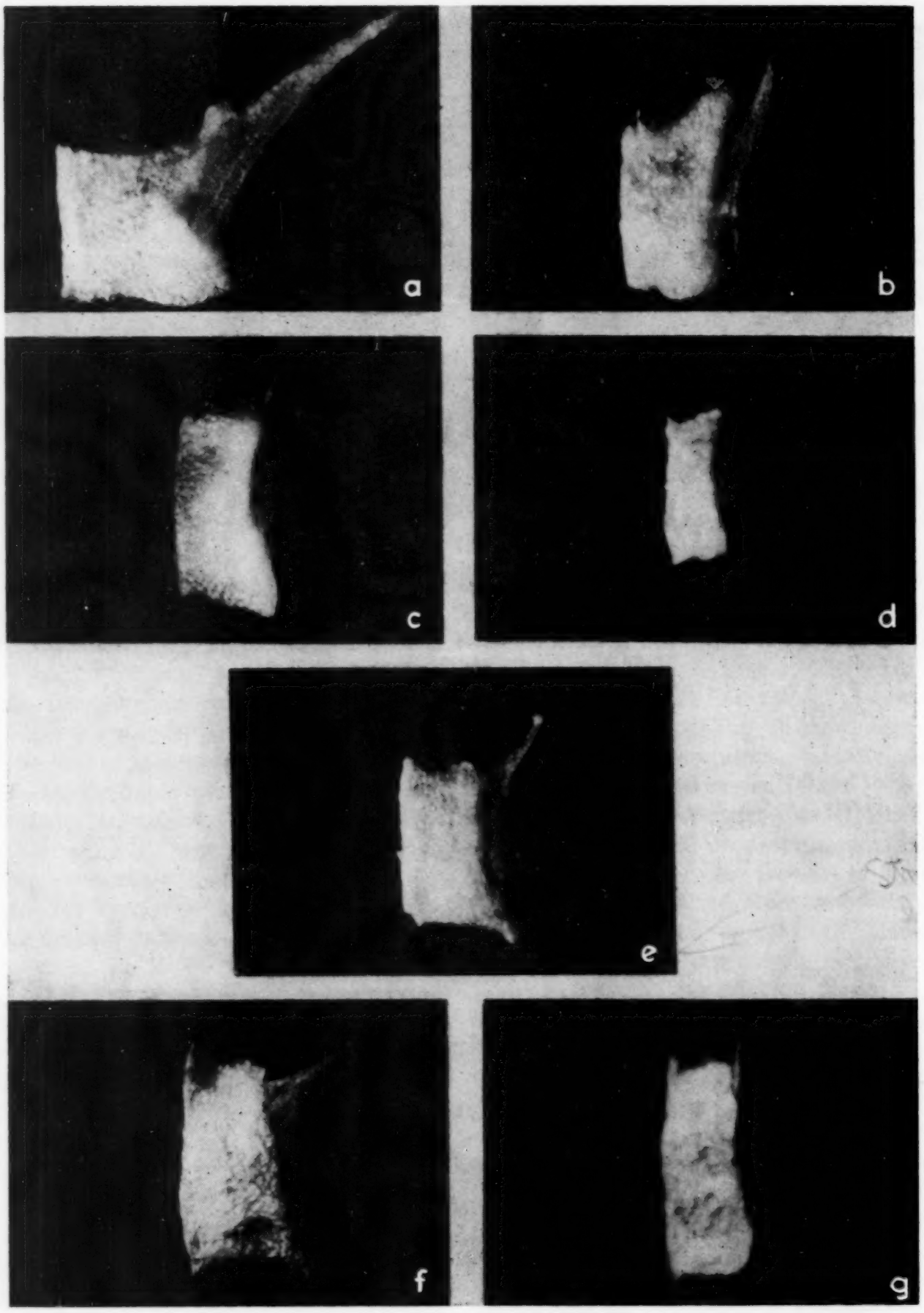

FIG. 8. Achenes of Maxwell Biotypes, along with artificial *M. sessilis* × *M. m. filiformis* F1 and F2 hybrids. (a) Achene of *M. sessilis* (14508#6), × 20. (b) Achene of *M. s. alopecuriodes* (14510#7), × 20. (c) Achene of *M. m. apus* (14510#X), × 20. (d) Achene of *M. m. filiformis* (14509#1), × 20. (e) Achene of F1 hybrid, *M. m. filiformis* × *M. sessilis* (jj#1), × 20. (f) Achene of F2 hybrid, *M. m. filiformis* × *M. sessilis* (jj–1#17), × 20. (g) Achene of F2 hybrid, *M. sessilis* × *M. m. filiformis* (ee–1#13), × 20.

artificial hybridizations between *M. sessilis* and *M. m. filiformis*. Using both the emasculation and mass-pollination techniques, six crosses (table 3) yielded F_1 hybrids with less than 5% pollen abortion and normal seed set. As had been previously demonstrated (Stone, 1957) meiotic pairing in both parents was normal

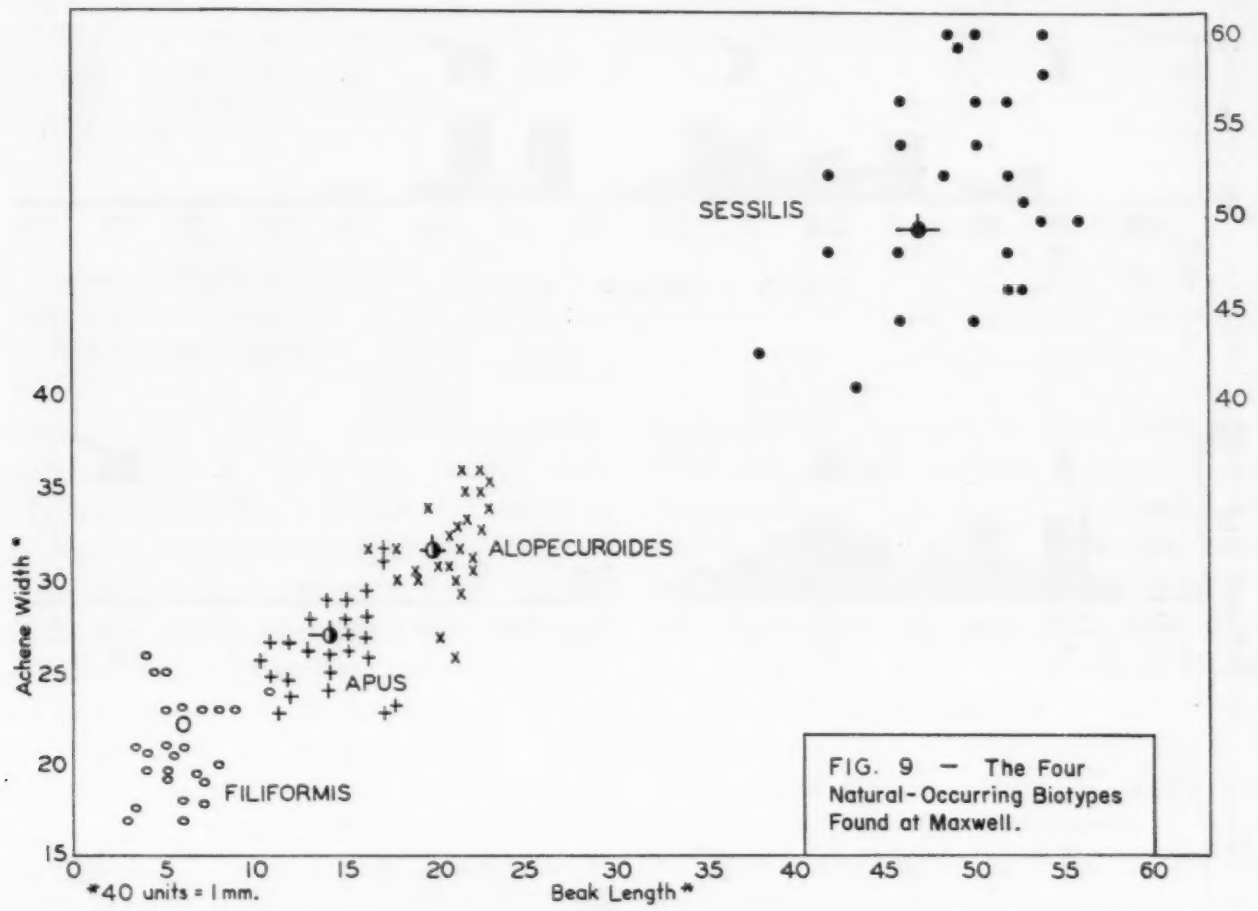

FIG. 9 — The Four Natural-Occurring Biotypes Found at Maxwell.

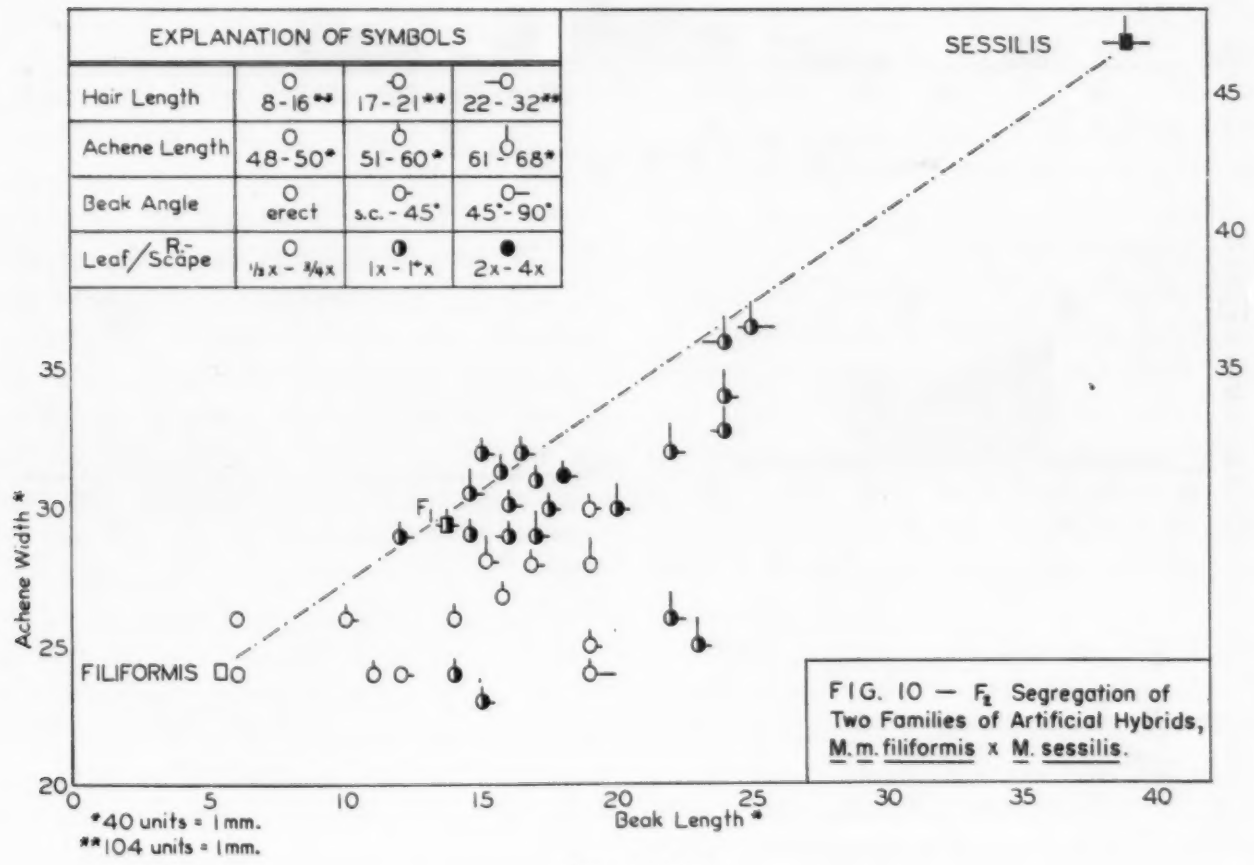

FIG. 10 — F_2 Segregation of Two Families of Artificial Hybrids, M. m. filiformis x M. sessilis.

FIGS. 9–10.

(n = 8, and 2n = 16), and the same was found to be true in the F_1's investigated.

The first point of interest has been concerned with the possibility of synthesizing individuals that approach the morphological intermediates found in nature. The scatter diagram in figure 10 (after Anderson, 1949) graphically displays the

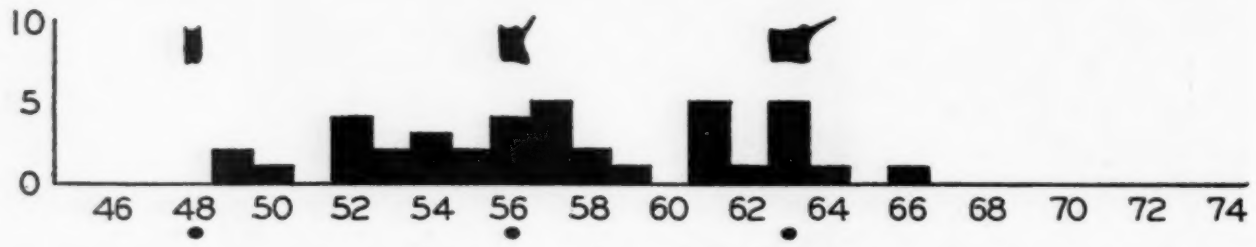

Fig. A — Achene Length *

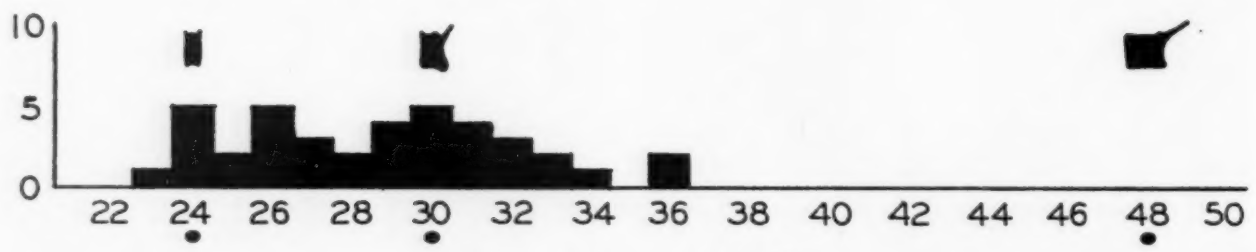

Fig. B — Achene Width *

Fig. C — Beak Length *

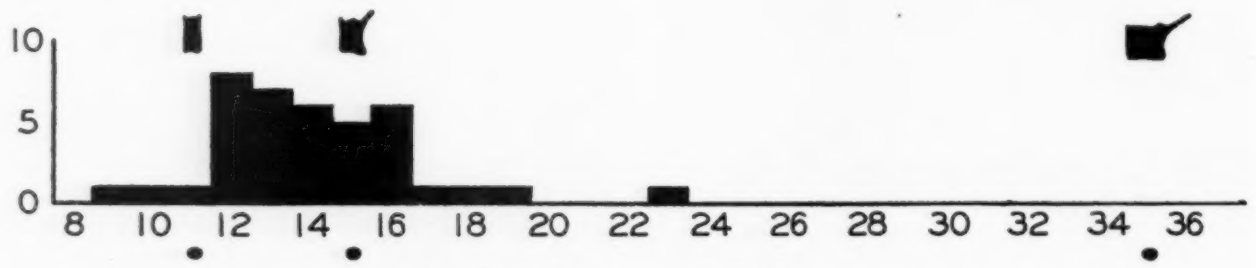

Fig. D — Hair Length **

FIG. 11. Frequency diagram of F2 segregating progeny of reciprocal cross between *M. m. filiformis* and *M. sessilis.*

TABLE 3. *Maxwell intra-population hybridizations*

Code	♀	♂	F1—Pollen good	F1—Abortion bad %	F1 seed set
M. m. filiformis × *M. sessilis*					
(1)	(9–1#1) ×	(1–8#1)	—	— 5*	Normal
(y)	(9–1#8) ×	(1–8#1)	—	— 0*	Normal
(jj)	(7–13#5) ×	(1–22#X)	185	0 0	Normal
(pp)	(7–7#1) ×	(1–22#X)	202	3 2	Normal
M. sessilis × *M. m. filiformis*					
(x)	(1–8#1) ×	(9–1#6, 9–1#9)	—	— —	Normal
(ee)	(1–8#5) ×	(7–13#2)	—	— —	Normal

* Estimate by inspection

correlated segregation of two combined populations of F_2 progeny (ee#1, and jj#1, see table 3). These F_2 progeny exhibited a considerable amount of segregation and in the case of achene length, leaf/recepto-scape ratio, and the beak angle, individuals as extreme as the parental types were occasionally recovered. Other characters such as achene width, beak length, and hair length do not approach the *M. sessilis* parent, but are distributed around the F_1 means and overlap with the *M. m. filiformis* parent (fig. 11).

The coincidence of the close proximity of the intermediate biotypes to *M. m. filiformis* on both the imaginary and real recombination spindle (figs. 9 and 10, respectively) is considered as additional support of the hybrid origin of the intermediate *M. s. alopecuroides* and *M. m. apus* biotypes. Furthermore, of the 36 F_2 progeny represented on the diagram (fig. 10), two individuals are characterized by the absence of hairs on the lateral faces of the achenes (see fig. 8f for an example), a condition previously known only in the *M. s. alopecuroides* biotype from Maxwell. Still other F_2's approach the *M. m. apus* biotype (fig. 8g). While the F_2's do not exactly duplicate the two morphological intermediates from Maxwell, this close approximation suggests that only additional selection in future generations would be necessary to give nearly identical biotypes. Perhaps even more striking is the large array of greenhouse-grown segregates, from both artificial and natural hybridizations, that are unknown in nature at Maxwell, but which are very similar to biotypes found in distant populations. One example is concerned with an unusual speckling of the seeds (fig. 6b), a condition known only in a single biotype of the Byron population (*M. sessilis*[1]) and some of the natural hybrids from Maxwell that were grown in the greenhouse. Interestingly enough some of these natural hybrids from Maxwell exhibited not only a similar speckling, but also resembled the Byron biotype in almost every other character.

Population analyses. The *Byron population* is situated in a series of poorly defined pools about three miles south of Byron (see fig. 1), at the western edge of the San Joaquin Valley. Depressions are common along the highway in untilled fields that are composed of a Solano silty-clay which impedes drainage. Although no hard-pan is present at Byron, a high water table and high evaporation rate successfully act in the formation of pools with a moderately to highly alkaline soil (table 1).

There is little question that the Byron population is the most complex of the colonies studied. Nine biotypes have been recognized (fig. 12), although further study will probably show that even more true-breeding families exist. The most difficult phase of the analysis has been in

reconciling the lush and giant mouse-tails of the 1952 collections with the dwarfed individuals collected in subsequent years. Even though the greenhouse helped standardize the phenotypic expressions of selected families of progeny, the majority of the field individuals were not progeny tested; therefore, it was difficult to be

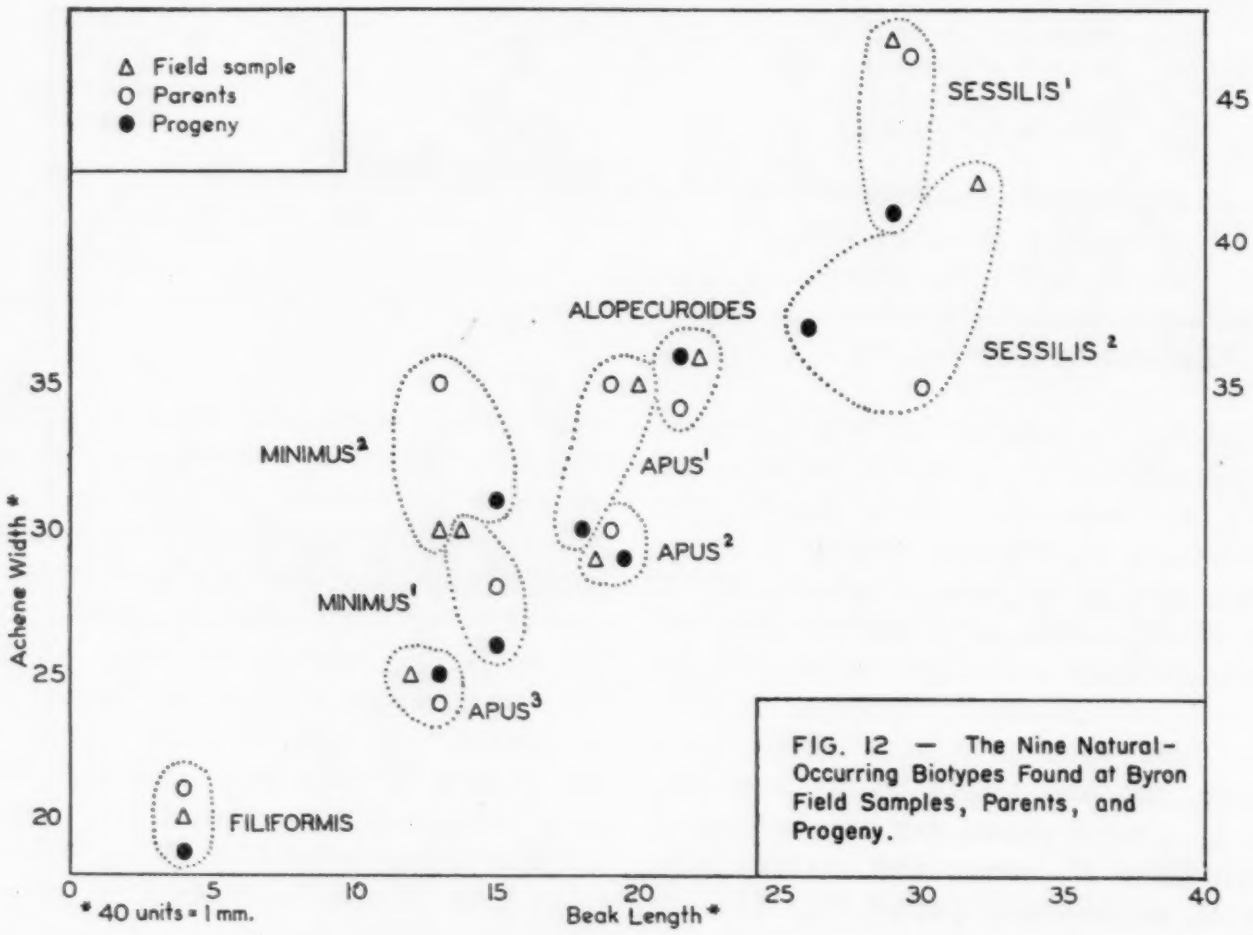

FIG. 12 — The Nine Natural-Occurring Biotypes Found at Byron Field Samples, Parents, and Progeny.

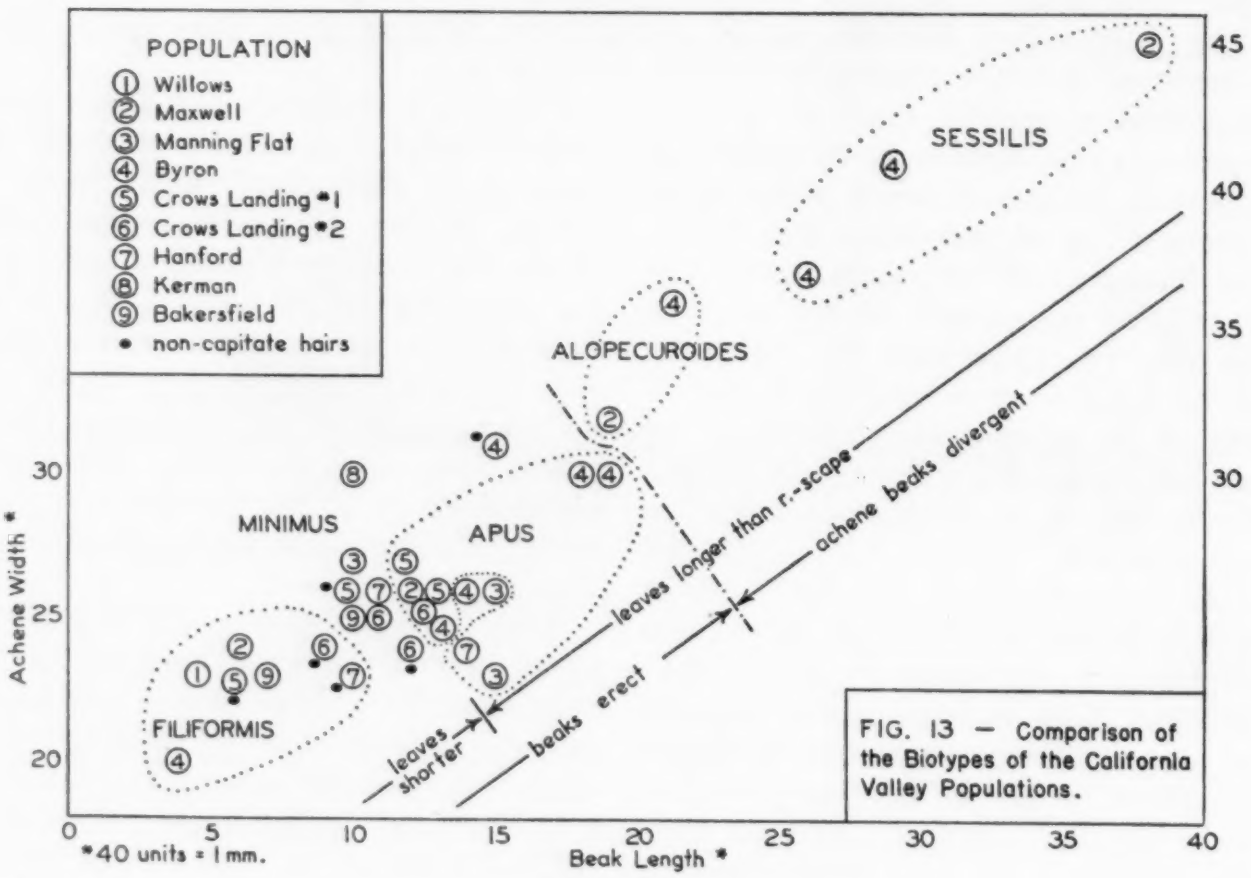

FIG. 13 — Comparison of the Biotypes of the California Valley Populations.

FIGS. 12–13.

sure if a minor morphological variant was due to environmental modification or a different genetic constitution.

Even though field samples were often similar in most respects (note *M. minimus*[1] and *M. minimus*[2]), progeny tests often suggested differences that were later confirmed by an intensive search for qualitative differences. In the case of these two biotypes of *M. minimus,* one group (*M. minimus*[1]) possessed the normal capitate achene hairs (fig. 6c), while *M. minimus*[2] had the unusual condition of smooth-tipped achene hairs (fig. 6d). As in the Maxwell population, the biotypes at Byron can be arranged on a scatter diagram that approximates a recombination spindle. Such a pattern is again reminiscent of the origin of intermediates through hybridization, elimination of a host of unfit segregates, and inbreeding leading to stabilization.

Inter-population comparisons. As a result of extensive progeny tests of biotypes from nine California Valley populations, it has been possible to compare groups of individuals on a common environmental background (see fig. 13). Certain populations (e.g. Willows) displayed but a single biotype, while others had as many as four (Maxwell, Crows Landing #1, and #2), or even nine (Byron) sympatric groups. As before, using achene width and beak length as coordinates for a scatter diagram, the biotypes fall on an imaginary spindle that extends from the long-peduncled, erect-beaked *M. m. filiformis* group to the short-peduncled, divergent-beaked *M. sessilis.*

Delimiting the species has necessarily been somewhat arbitrary, especially since the biotype series is quite complete, with but few discontinuities. Nevertheless, certain biotypes can conveniently be grouped and considered as part of a single taxon. Utilizing beak curvature one can recognize two groups of mouse-tails: the curve-beaked *M. sessilis* and *M. s. alopecuroides* group and the straight-beaked *M. minimus* complex. *Myosurus sessilis* characteristically has a much reduced peduncle and long leaves (2–4 × the recepto-scape), while *M. s. alopecuroides* has a conspicuous peduncle (more than 20 mm.) and leaves 1–2 × recepto-scape. The three erect-beaked groups are subdivided into those which have leaves longer than the recepto-scape (*M. m. apus*) and those which have leaves shorter than the recepto-scape (*M. m. filiformis* and *M. minimus*). The fine distinction between these latter two groups is mainly one of achene size: the *M. m. filiformis* group has short achene beaks, achene bodies, and achene hairs, along with narrow achenes (long sepal spur also present); *M. minimus* has somewhat larger achenes in all respects in addition to a shorter sepal spur. The peculiar non-capitate hair type has been found only in certain biotypes of *M. minimus* and *M. m. filiformis,* indicated by the dot (●) in figure 13.

The morphological characters of individuals are highly correlated with the position of the biotype dot on the spindle. That is to say, biotypes near the lower end of the spindle have short achene hairs, low sepal blade/spur ratios, etc., while biotypes approaching the upper limit (near *M. sessilis*) have long achene hairs, high sepal blade/spur ratios, etc.

While the northern populations (i.e. Maxwell and Byron) of *Myosurus* may contain a wide variety of biotypes ranging from one end of the spindle to the other, the absence of curve-beaked biotypes in the southern localities is striking. Although exceptions occur, the populations of the three dominant taxa (*M. sessilis, M. m. apus,* and *M. m. filiformis*) follow a north-south distribution which agrees with their gradient in external morphology. *Myosurus sessilis,* the biotype with curved beaks and short peduncles, has a northern distribution in the Great Valley of California, while *M. m. apus,* with straight beaks and intermediate length peduncles, is concentrated in the central to southern end of the valley. *Myosurus m. filiformis* with straight beaks and long peduncles is scattered throughout the val-

ley, but extends as far south as Baja California and Guadalupe Island. In order to account for the distribution of the putative hybrid biotype of *M. m. apus,* two speculations are warranted. First, it is possible that the point of contact between *M. sessilis* and some form of *M. minimus* occurred in approximately the same area as that where they overlap today. If this were the case, the intermediate *M. m. apus* has moved south since its origin. The second possibility is that the present day distribution of *M. sessilis* is but a shadow of its past widespread occurrence throughout California. Hybridization and elimination of *M. sessilis* in the southern end of the valley could have led to distribution patterns not very different from that found today. The other putative hybrid, *M. s. alopecuroides,* is known only from a few localities in the Sacramento Valley area, ranging from Maxwell in the north to Byron in the south. Its occurrence coincides with its present day, restricted association with *M. sessilis;* thus pointing to this endemic area as its probable center of origin.

Discussion

As recognized by Clausen (1951) the local population is the basic evolutionary unit in the gradual process of differentiation or speciation. Each local group of individuals which is spatially isolated from a nearby population functions as a more or less independent unit. In the case of the predominately inbreeding mouse-tails, each population is characterized by distinct biotypes which have responded to the conditions peculiar to "hog-wallows" of a particular area. Self-fertilization, spatial isolation imposed by restricted conditions suitable for vernal pools, and local edaphic conditions are the most important factors operating in assuring local adaptation and differentiation.

While the action of natural selection on the potential biotypes is a strong force in determining the composition of a population, it is relegated to a secondary role. This implies that before selection comes into play, the factors initiating population differentiation (i.e. mutation and recombination) set the limits for selection, and in doing so channel its direction. The surviving biotypes which will characterize the taxon will be a reflection of the parental types and the interaction of their hybrid progeny with forces of natural selection. In some cases similar ecological niches in disjunct populations will favor the spread of a well adapted type, such as the *M. m. apus* group found at Byron, Crows Landing, and southward to San Diego. More often, however, the highly specialized conditions and fluctuations of these conditions within a population will demand a new variant which is just a little better fitted than any existing type.

The evidence favoring intra-population speciation leads to some interesting conclusions. The implication is that certain groups of biotypes which can be given specific or subspecific rank are actually related through an indirect lineage of descent. That is to say, the biotypes may actually be related through independent hybridization of similar parental types. Comparisons of the putative parents in both the Maxwell and Byron populations show inter-population differences which are reflected in the putative hybrids. *Myosurus s. alopecuroides* at Maxwell has a divergent beak (45°), intermediate between the 90° and 0° putative parental extremes, while *M. s. alopecuroides* from Byron has a beak divergence around 20°, also intermediate between the putative *M. sessilis* and *M. minimus* parents.

Corroborative evidence on the factors influencing population structure show that the breeding system which will give a picture of population mosaicism is not limited to a specific pattern of isolation, but can have devious ways of producing similar results. Of the more intensively studied species which exhibit the pattern of sympatric differentiation (see also Straw, 1955; Dunn, 1956; and Fryxell, 1957), self-fertilization played an important role in the following groups: *Erophila* (Winge, 1940); *Bromus* (Harlan, 1945);

Microseris (Chambers, 1955); and *Stellaria* and *Senecio* (Haskell, 1949, 1954).

It would seem at first glance that a balanced breeding system is suited to cope with most any situation that might develop, as stability and flexibility are inherent features. While this type of evolution has been successful in many instances, its short-comings in annual plant species are inevitable as a result of the restriction of gene exchange and the reduction in the potential reservoir of variability. In fact, as suggested by Chambers (1955), further restrictions to outcrossing, in the light of the isolating effect of self-pollination in annual plants, would be undesirable.

The practical model of the inbreeding-outbreeding system, as outlined above, has suggested certain theoretical conclusions which agree quite closely with studies in the vernal-pool *Myosurus*. As Wright (1956) emphasized, "in nature, the conditions are continually changing," and thus have profound effects on the "goal of selection" and the pattern of adaptation. Changing environments influence the hybridity equilibrium in establishing the effective system which must meet the demands of selection. While the selection in clones is extremely effective, only the recombination through outcrossing (or a mutation rate correlated with a high reproductive capacity) offers the store of variability for adaptive changes. One such compromise, which increases the efficiency of selection while not binding the population to a single adaptive peak, is the alternation of a predominant inbreeding system with occasional outcrossing. Wright pictures this system as one of "violent alterations" in which adaptive biotypes are broken down through hybridizations in the production of new combinations. "It is a system that is probably more significant as a means of insuring the appearance of adaptive genotypes, capable of taking advantage of any temporary bonanza, whatever the special conditions, than of progressive evolution" (Wright, 1956, p. 16).

Summary

A study of some nine California Valley populations of *Myosurus* uncovered an array of sympatric biotypes, some of which showed signs of intermediacy between two morphological extremes, *M. sessilis* Wats. and *M. m. filiformis* Greene. The isolating mechanism responsible for reduced outbreeding was found to be associated with the peculiar development of the ranunculaceous flower. In *M. sessilis* the stamens hover over the pistil-bearing receptacle at the time of anthesis and thoroughly self-pollinate the flower; however, under favorable growing conditions the receptacle continues to elongate and develop new pistils at the tip. The other sympatric morphological extreme, *M. m. filiformis,* has appressed sepals and stamens about one half as long as the receptacle at anthesis. Thus pollination will be affected on the lower half of the receptacle, while the upper portion protrudes above the sepal enclosure, free and clear of the released pollen. While the lower portions of the receptacles are self-pollinated, the unfertilized upper pistils offer the chance for occasional outbreeding. The fact that a single flower can produce both inbred and outbred seed is considered to be quite unique.

Sampled populations throughout the Great Valley of California display in some cases as many as four, five, or even nine true-breeding, sympatric biotypes. In at least two populations, Maxwell and Byron, two extreme morphological biotypes are found, *M. sessilis* and *M. m. filiformis,* along with a host of morphologically-intermediate, true-breeding entities. It has been suggested that the intermediate [*M. s. alopecuroides* (Greene) Stone, and *M. m. apus* (Greene) Campbell] arose by chance hybridization, and as a result of selection and continued inbreeding stabilized biotypes resulted. Artificial hybridizations tend to confirm this hypothesis and lend support to the idea that other similar intermediate biotypes throughout California had a similar hybridization impetus.

The accumulated evidence suggests that the balanced inbreeding-outbreeding system in *Myosurus* is particularly well adapted for fluctuating environmental conditions. A hybridity equilibrium weighted on the side of inbreeding insures both fitness—through homozygous seed production, and flexibility—through occasional chance hybridizations that may become established by repeated self-fertilizations and selection.

Acknowledgments

It is with great appreciation that I wish to thank the members of the Departments of Botany and Genetics at the University of California at Berkeley. Special thanks goes to Professor Herbert L. Mason for his guidance and suggestion of problems in the mouse-tails, and to Professor G. Ledyard Stebbins for his inspiration in the evolutionary aspects of the problem. A final note of heartfelt thanks is due to my wife, Beverly L. Stone, who has served as artist, typist, and critic.

Through the generous cooperation of Professor Herbert L. Mason and the University of California Press (MARSH FLORA, Mason, 1957) it has been possible to reproduce one of the exquisite plates drawn by Mary Barnas Pomeroy (figs. 5a–5g).

Literature Cited

Anderson, E. 1949. Introgressive hybridization. Wiley and Sons, New York. 109 pp.

——, and G. L. Stebbins. 1954. Hybridization as an evolutionary mechanism. Evolution, **8**: 378–388.

Baker, H. G. 1953. Race formation and reproductive method in flowering plants. Symposia of Soc. Exp. Biol., **7**: 114–145.

Chambers, K. 1955. A biosystematic study of the annual species of *Microseris*. Contr. Dudley Herb., **4**: 207–312.

Clausen, J. 1951. Evolution of plant species. Cornell Univ. Press, New York. 206 pp.

Crosby, J. L. 1949. Selection of an unfavorable gene-complex. Evolution, **3**: 212–230.

Darlington, C. D., and K. Mather. 1952. The elements of genetics. Allen and Unwin, London. 446 pp.

Dunn, D. B. 1956. The breeding systems of *Lupinus*, group Micranthi. Amer. Mid. Nat., **55**: 443–472.

Fryxell, P. A. 1957. Mode of reproduction of higher plants. Bot. Rev., **23**: 135–233.

Grant, V. 1949. Pollination systems as isolating mechanisms in angiosperms. Evolution, **3**: 82–97.

——. 1952. Isolation and hybridization between *Aquilegia formosa* and *A. pubescens*. El Aliso, **2**: 341–360.

Harlan, J. R. 1945. Natural breeding structure in the *Bromus carinatus* complex as determined by population analyses. Amer. Journ. Bot., **32**: 142–148.

Harris, F. S. 1920. Soil alkali. Wiley and Sons, New York. 258 pp.

Haskell, G. 1949. Variation in the number of stamens in the common chickweed. Journ. Genetics, **49**: 291–301.

——. 1954. Adaptation and the breeding system in groundsel. Genetica, **26**: 468–484.

Hoover, R. F. 1937. Endemism in the flora of the Great Valley of California. Ph.D. Thesis, Univ. of Calif., Berkeley.

Kelley, W. P. 1951. Alkali soils. Rheinhold Publishing Corp., New York. 176 pp.

Knuth, P. E. 1906. Handbook of flower pollination. I. Introduction and Literature. Translated by J. R. Davis. Clarendon Press, Oxford. 382 pp.

——. 1908. Handbook of flower pollination. II. Observations on flower pollination. Translated by J. R. Davis. Clarendon Press, Oxford. 703 pp.

Mason, H. L. 1957. A flora of the marshes of California. University of California Press, Berkeley. 878 pp.

Müller, H. 1883. The fertilisation of flowers. Translanted by D. W. Thompson. Macmillan and Co., London. 669 pp.

Stebbins, G. L. 1950. Variation and evolution in plants. Columbia University Press, New York. 643 pp.

——. 1957. Self fertilization and population variability in higher plants. Amer. Nat., **91**: 337–354.

Stone, D. E. 1957. Studies in population differentiation and variation in *Myosurus* of the Ranunculaceae. Ph.D. Thesis. Univ. of Calif., Berkeley.

Straw, R. M. 1955. Hybridization, homogamy, and sympatric speciation. Evolution, **9**: 441–444.

Winge, O. 1940. Taxonomic and evolutionary studies in *Erophila* based on cytogenic investigations. Comp. Rend. Lab. Carlsberg, **23**: 41–74.

Wright, S. 1931. Evolution in mendelian populations. Genetics, **16**: 97–159.

——. 1956. Modes of selection. Amer. Nat., **90**: 5–24.

NASAL ANATOMY AND THE PHYLOGENY OF REPTILES

THOMAS S. PARSONS

Harvard Biological Laboratories, Cambridge 38, Mass.

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INTRODUCTION

In the course of research on the embryology of the reptilian nose, I concluded that the structure and development of the nasal cavities in various recent tetrapods might give some clews to the phylogeny of the major groups of reptiles. The detailed results of this research are being published elsewhere (Parsons, in press), but it seems advisable to consider the major phylogenetic implications separately, without burying them in a mass of descriptive data; such is the aim of this paper.

The division of the class Reptilia into major subgroups and the relationships between such subgroups have long been subjects of debate in the literature. On the basis of the anatomy of the heart and aortic arches, Goodrich (1916) proposed dividing the reptiles into the sauropsids, comprised of all the living orders of reptiles and their fossil relatives including the ancestors of birds, and the theropsids, those groups of extinct reptiles which are related to the ancestry of mammals. His views have been widely accepted by many workers, especially Watson (1951–1957) who has utilized the anatomy of the middle ear as further evidence for the separation of sauropsid and theropsid reptiles. However other authors have been impressed with the differences between turtles and all other recent groups. The most important paper stressing these differences, especially those in the skull, is that of Olson (1947), who divides the reptiles into the Parareptilia (turtles and fossil relatives) and the Eureptilia (all other reptiles, including the other recent reptilian orders and the ancestors of both birds and mammals).

Obviously in any subject of disagreement such as this, more evidence is needed. Nasal anatomy appears to offer some assistance, and is therefore of considerable interest.

Although detailed anatomical descriptions are beyond the scope of this paper, a brief outline of the major features of each group is included before the more detailed consideration of the phylogenetic implications. The following section is essentially a rather extensive footnote or appendix presenting a summary of the data on which the remainder of this paper is based. More complete anatomical descriptions and many references to the literature may be found in the works of Matthes (1934) and Parsons (in press). Major papers on the olfactory bulbs and neural connections of the nose include those of Zuckerkandl (1910), Herrick (1921), and Crosby and Humphrey (1939). All the observations summarized below are taken from these works or works cited in them.

I am indebted to Drs. Ernest E. Williams and Alfred S. Romer of Harvard University for their many helpful suggestions and comments concerning this subject, and to Drs. Williams and Ernst Mayr for kindly reading the manuscript for me. Finally my thanks are due to Mrs. Thomas S. Parsons for assistance in the preparation of the manuscript and, especially, the illustrations.

NASAL ANATOMY OF RECENT GROUPS

Urodela: The modern urodeles show considerable variation in their nasal anatomy. Much of this variation occurs in the neotenous forms; however since the interpretation of their nature is a major problem in itself, they are not treated here. In most fully metamorphosed forms, such as *Triturus* (fig. 1A), the nasal

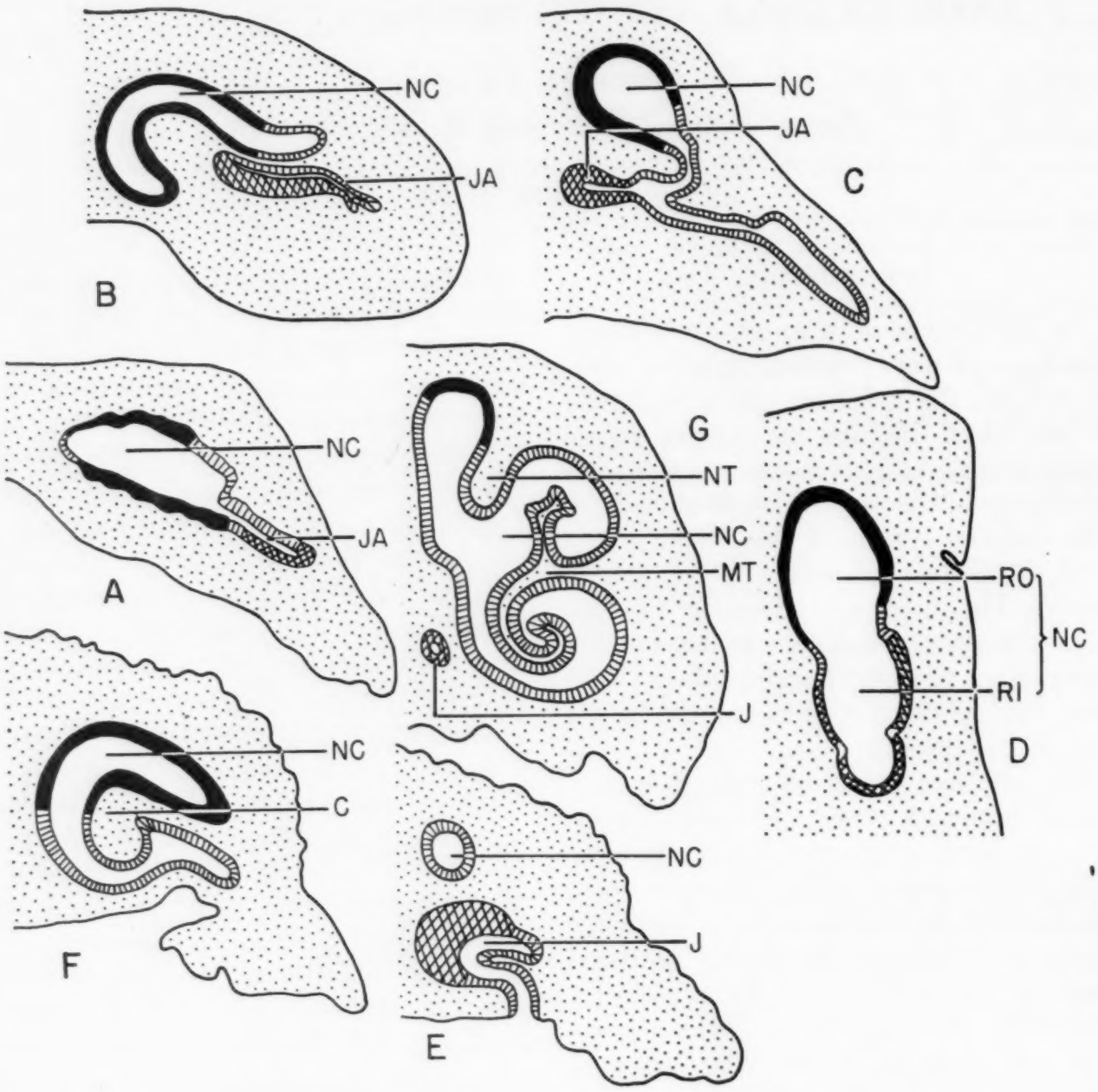

FIG. 1. Transverse sections through the nasal cavities of various forms. A, *Triturus;* B, *Ichthyophis;* C, *Hyla;* D, *Emys;* E, *Phyllodactylus,* anterior part of nose; F, *Phyllodactylus,* posterior part of nose; and G, *Talpa.* Sensory olfactory epithelium containing Bowman's glands is solid black, sensory olfactory epithelium lacking Bowman's glands is cross-hatched, and non-sensory nasal epithelium is lined. Abbreviations: C, concha; J, Jacobson's organ; JA, "Jacobson's organ" of amphibians; MT, maxilloturbinal; NC, nasal cavity; NT, nasoturbinal; RI, regio intermedialis; and RO, regio olfactoria. (A and D after Seydel, B after Sarasin and Sarasin, C and G after von Mihalkovics, and E and F after Fuchs.)

chamber is a very simple cavity which appears roughly oval in transverse section. There is a narrow groove extending laterally from the ventrolateral corner of the main chamber; this groove is the so-called "Jacobson's organ." Sensory olfactory epithelium lines the greater part of the main nasal chamber, occurring on the dorsal, medial, and ventral walls. Throughout this sensory area there are numerous small flask-shaped glands, the Bowman's glands or glandulae olfactoriae. Another area of sensory epithelium, which differs from the first in being completely devoid of Bowman's glands, occurs in the wall of the ventrolateral groove, as shown in the figure.

Fibers of the olfactory nerve arise from both sensory areas, and run to the anterior end and lateral surface of the olfactory bulb (fig. 2A). All the fibers from the ventrolateral sensory area pass around the ventral side of the nasal cavity in their course towards the bulb, and they tend to enter the lateral surface of the latter structure posterior to the points of entrance of most of the nerve fibers from the larger medial sensory area of the nose. The posteriormost part of the olfactory bulb which receives primarily fibers from the lateral sensory area is often termed the accessory olfactory bulb; however it is not, in urodeles, distinctly separated from the remainder of the

bulb, nor does it receive exclusively fibers from the lateral sensory area of the nose.

Gymnophiona: In the gymnophionans or caecilians the nasal cavity has a more complex form, as shown in figure 1B. The main nasal chamber is falciform in transverse section with the concave side ventral. A small digitiform extension of the nasal cavity extends anteriorly and laterally from the anterolateral corner of the internal naris or choana, and is generally termed "Jacobson's organ." The medial two-thirds of the main chamber and the ventral surface of the small diverticulum bear sensory epithelium; the former area possesses Bowman's glands and the latter does not.

As in the urodeles, the two sensory areas both give rise to olfactory nerve fibers, and the fibers from the ventrolateral sensory area pass ventral to the nasal cavity in their path to the brain. However there are differences in the olfactory bulb. In gymophionans the small posterior part generally believed to receive the fibers from the "Jacobson's organ" (the nerve has not been much studied in any member of this group) forms a distinct area which may be sharply separated from the remainder of the olfactory bulb. Thus there is present a distinct accessory olfactory bulb. It lies posterior to the dorsolateral part of the main bulb, at least in *Ichthyophis.*

Anura: Frogs and toads possess the most complex nasal cavities of any modern amphibians. As shown in figure 1C (*Hyla*), the main nasal chamber is, when seen in transverse section, an extensive round cavity. Ventral to this chamber and connected to it by a narrow slit-like opening, there is a large subsidiary cavity which extends laterally and, in the anterior half of the nasal region, also medially. The main (dorsal) nasal chamber is lined by sensory epithelium which contains Bowman's glands; in the ventral cavity sensory epithelium is typically present only medially. The latter region contains no Bowman's glands, and is generally termed "Jacobson's organ."

The olfactory nerves and bulbs of anurans resemble closely those of the gymophionans, and only two differences need to be noted. First, since the only sensory epithelium of the "Jacobson's organ" is on the medial wall of the nose, its nerve fibers do not pass ventral to the nasal cavity, but merely run posteriorly to reach the accessory olfactory bulb. Secondly, the accessory olfactory bulb is, in *Rana* at least, ventrolateral rather than dorsolateral in position.

Chelonia: The nasal cavities of turtles differ radically from those of all other reptiles, and resemble more closely those of amphibians, especially urodeles. In a form such as *Emys* (fig. 1D), the cavity appears oval when seen in transverse section. Two roughly equal halves

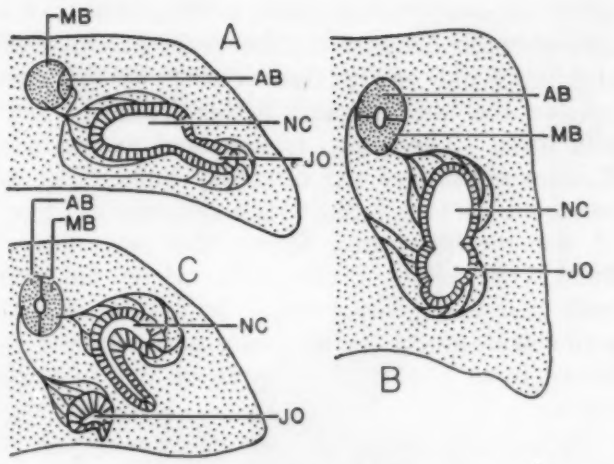

FIG. 2. Diagrams of the nasal areas of various forms to show the innervation of the nose. In order to show the nasal cavities in transverse section, the olfactory bulbs are figured as lying dorsomedial to the center of the nasal cavity; actually they are well posterior to this position. The distinctness of the two main subdivisions of the olfactory nerve is considerably exaggerated, especially in A. A, a urodele; B, a turtle; and C, a snake. Abbreviations: AB, accessory olfactory bulb;; JO, Jacobson's organ or its probable homolog; MB, main olfactory bulb; and NC, nasal cavity. The solid lines represent the branches of the olfactory nerve.

may be distinguished; dorsally there is a chamber lined with sensory epithelium containing Bowman's glands and ventrally one partially lined by sensory epithelium which lacks such glands. These have generally been termed the pars olfactoria and the pars respiratoria or Jacobson's organ respectively, but, for reasons explained elsewhere (Parsons, in press), may better be called the regio olfactoria and regio intermedialis. In forms such as the one figured, the sensory epithelium of the regio intermedialis occurs as three parallel bands along its walls, one medial, one ventral, and one lateral.

There is considerable variation in the nasal cavities of recent turtles, and two other patterns must be briefly noted. First, in *Testudo,* the lateral wall of the regio olfactoria is convex and bulges into the nasal cavity. Another peculiarity of *Testudo* is the restriction of the sensory epithelium of the regio intermedialis to the medial wall. The other major variant pattern is that seen in the sea turtles. These forms possess only a small regio olfactoria which is posterodorsal in position, while the regio intermedialis occupies the anteroventral three-quarters of the nasal cavity. The sensory epithelium of the latter region is restricted to two pockets, one located anteroventrally and the other anterodorsally.

In all turtles thus far studied, the olfactory nerve arises from the sensory epithelium of the nose and forms two major groups of bundles,

often referred to as trunks (fig. 2B). The medial trunk arises from the regio intermedialis and its distal end passes ventral to the nasal cavity; the lateral trunk arises from the regio olfactoria. These two trunks lead to two very distinct regions of the olfactory bulb. The accessory olfactory bulb, which receives the fibers of the medial trunk, forms the posterodorsal third (roughly) of the bulb, while the main bulb comprises the ventral half plus the anterior end of the entire bulb, and receives the fibers from the lateral trunk of the olfactory nerve.

Before describing the nasal anatomy of the remaining groups, some consideration of the embryology of the nasal cavities is necessary. Unfortunately little can be said concerning the amphibians; although they have often been studied, the descriptions of their nasal development show marked disagreement on most points. Space does not permit any review of this involved topic here. However, all amniotes share certain features of nasal embryology which can be outlined briefly.

In all amniotes the nose first appears as a thickening of the epidermis of the snout, the nasal placode. This soon invaginates to form the nasal pit. The lateral and medial walls of this pit, the lateral and medial nasal processes, grow ventrally, and finally fuse at their ventral ends. Fusion does not occur throughout the length of the nasal pit, but only ventral to its center. Thus the anterior end of the primitive naris, or opening to the nasal pit, remains open as the external naris, and similarly its posterior end forms the choana or internal naris. In mammals, the latter opening is secondarily closed by the formation of the bucconasal membrane which ruptures in later developmental stages.

Two other features are common to all amniotes except turtles; these are shown in figure 3. One of them is the formation of a typical Jacobson's organ from an inpocketing of the ventromedian wall of the nasal pit. Such an inpocketing first forms shortly before the fusion of the nasal processes mentioned above, and is found even in those groups which lose Jacobson's organ in the adult. A comparison of figure 3A (a turtle) with 3C, 3E, and 3G (a snake, a crocodile, and a human) demonstrates the complete absence of this inpocketing in turtles and its similarity in other and diverse amniotes. In all those forms in which a typical Jacobson's organ is found, the ventral wall of the nasal cavity lacks sensory epithelium, and the only sensory olfactory epithelium which lacks Bowman's glands is found in Jacobson's organ. In all cases where it persists in the adult, Jacobson's organ gives rise to a special medial trunk of the olfactory nerve which runs to an accessory olfactory bulb basically similar to that found in turtles (fig. 2C).

The other feature common to most amniote embryos is the formation of the concha, a process of the lateral nasal wall which extends out into the nasal cavity. As shown in figures 3D, 3F, and 3H, the concha first appears soon after the fusion of the nasal processes; however in turtles (fig. 3B) it is lacking. Some authors have tried to find a homolog for the concha in the chelonian nose, and have proposed the convexity of the lateral wall of the regio olfactoria of *Testudo;* the fact that this convexity is prominent only in that form (of those studied), makes its interpretation as a specialization seem more probable. Other workers have suggested that the ridge on the lateral wall between the regiones olfactoria and intermedialis may be the concha, but that ridge bears no real resemblance to the concha of any other form.

Rhynchocephalia: In *Sphenodon* the nasal cavity remains relatively simple. The embryonic concha (described above) becomes the concha posterior in the adult, and another extension of the wall, the concha anterior, arises anteroventrally on the lateral nasal wall. Jacobson's organ remains a simple tubular pocket in the medial wall of the nose, at the anterior end of the choana. The small accessory olfactory bulb is dorsomedial in position in this form, and the main bulb receives all the olfactory nerve fibers from the main nasal cavity, the posterodorsal half of which bears sensory epithelium.

Squamata: In both lizards (figs. 1E and 1F) and snakes the main nasal cavity possesses only the single concha seen in the embryo; in some forms even this may secondarily be lost. As in *Sphenodon,* the posterodorsal part of the nasal cavity is sensory and the anteroventral is not. However in this order there has been a great development of Jacobson's organ which typically opens into the oral rather than the nasal cavity of the adult. The olfactory nerve and bulb resemble those of *Sphenodon* closely, differing only in the greater size and in the medial rather than dorsomedial position of the accessory olfactory bulb in most lizards and snakes.

Crocodilia: In crocodilians Jacobson's organ disappears completely at an early stage (compare figs. 3E and 3F), and an accessory olfactory bulb is not formed. However the main nasal cavity undergoes considerable modification. The embryonic concha becomes subdivided to form the preconcha and middle concha, and a third process, the postconcha, forms independently posterior to the others, thus producing a row of three extensions of the lateral nasal wall. Other new developments of less interest for this study include the formation of numerous paranasal sinuses and of a secondary

palate, so that the choana of the adult lies far posterior to its embryonic position. Sensory epithelium is restricted to the posterodorsal third to quarter of the nasal cavity.

Aves: Birds share with crocodilians several features of nasal anatomy which are presumably characteristics inherited from a common ancestor. These include the development of a

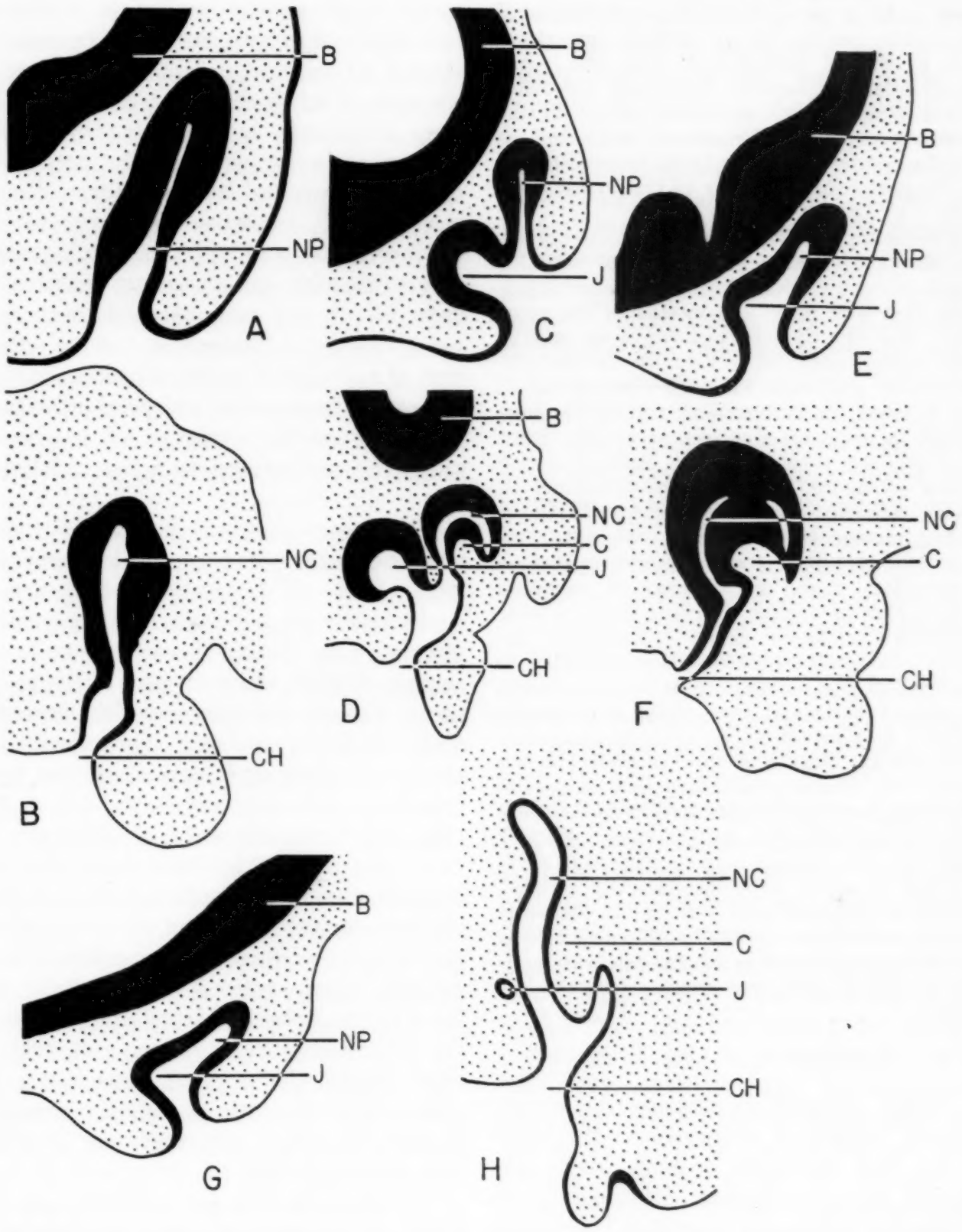

FIG. 3. Transverse sections through the nasal cavities of amniote embryos. A and B, *Chrysemys;* C and D, *Thamnophis;* E and F, *Crocodylus;* and G and H, *Homo.* A, C, E, and G show a stage shortly before the fusion of the nasal processes, and B, D, F, and H a stage shortly after their fusion. Abbreviations: B, brain; C, concha; CH, choana; J, Jacobson's organ; NC, nasal cavity; and NP, nasal pit. (E after Voeltzkow, F after Fuchs, and G and H after Arey, Developmental Anatomy, 6th ed., 1954, W. B. Saunders Co. by permission of publishers.)

postconcha and the loss of Jacobson's organ (although it is present in early embryonic stages) and of the accessory olfactory bulb. Birds also resemble crocodilians in possessing a third concha lying anteriorly on the lateral nasal wall; however it is not a subdivision of the middle concha, but an entirely new structure which had developed in this class. Another difference between birds and crocodiles is the absence of a secondary palate in the former group. Finally sensory epithelium is greatly restricted in most birds, occurring only on the posterodorsal corner of the lateral nasal wall.

Mammalia: The last group to be considered, the mammals, show a great range of variation which can only be touched upon here. Typically there are many outgrowths of the nasal wall. The first of these to form in the embryo (the concha in fig. 3H) becomes the maxilloturbinal of the adult (see fig. 1G); dorsal to this is found the nasoturbinal, and further posteriorly a series of ethmoturbinals. The latter structures are posterior to the plane of section shown in figure 1G. Sensory epithelium is, again, restricted to the posterodorsal region, mainly on the ethmoturbinals. Mammals, or their ancestors, have also independently evolved a secondary palate and a series of paranasal sinuses, thus paralleling the crocodilians in these features. Jacobson's organ is generally retained as a small digitiform organ connected to the roof of the mouth by the incisive canals. In some mammals it may retain its primitive position as a pocket off the ventromedian nasal wall, and in others it is lost completely in the adult. An accessory olfactory bulb is present whenever Jacobson's organ persists in the adult and lies posterodorsal to the main olfactory bulb. In some cases it may be somewhat medially and in others somewhat laterally situated. The entire olfactory bulb is shorter in mammals than in reptiles, and forms an olfactory lobe at the anteroventral corner of the cerebral hemisphere, but its structure remains basically the same.

Evolution of the Nose

In any attempt to describe the evolutionary history of an organ on the basis of its form in recent animals, there are several major problems. Presumably all successful forms are specialized to some degree; any animal must be adapted to its environment in order to survive. Thus functional considerations should always enter into an evolutionary discussion. However in the case of the nose, so little is known about its function that such considerations are, at the present time, impossible.

Another major problem is that of parallel evolution. In some cases structures which appear similar in adults of two different groups can easily be demonstrated to be independent acquisitions of the two. Such is the case when they arise very differently in the ontogeny of the groups, as is the case with the preconcha of crocodilians and the anteriormost concha of birds, or when the fossil record demonstrates an independent phylogenetic origin as with the secondary palates of crocodilians and mammals. However in most cases the picture is not so clear, and the decision as to whether or not structures have arisen independently must be based on the evidence of a general similarity as opposed to a few relatively minor differences.

The more closely related two forms are, the harder it becomes to recognize parallelism. This increased difficulty is undoubtedly caused in part by the greater general resemblance between two such forms; that is, there is less likely to be some radical difference which immediately indicates a basic dissimilarity of the two. Another factor which can contribute to this problem is the possibility that the resemblance in a structure in two groups may be caused by the inheritance from a common ancestor, not of the structure itself, but of the tendency to form it. In such a situation, other, equally closely related forms, might not have realized that tendency and thus lack the structure. Whether or not such a case should be termed parallelism is primarily a semantic argument; however it certainly does not represent a truly independent origin.

Turning then to the evolution of the nose, it appears to me that primitive tetrapods must have possessed two very distinct sensory areas in the wall of the nasal cavity. The larger one was dorsally located and contained Bowman's glands. These glands, which do not occur in fish, are found in the dorsal sensory epithelium

of every tetrapod with the exceptions of larval and neotenic amphibians and, possibly, one genus of sea snakes. The function of Bowman's glands is not known, but they are generally thought to be essential for olfaction by the dorsal sensory area in tetrapods (again, larval and nonmetemorphosed amphibians excepted). However ventrally or possibly ventromedially there was apparently a second sensory area in which such glands never developed. This ventral sensory area is frequently termed Jacobson's organ; however many authors prefer to restrict that term to those cases in which the organ forms as a ventromedial pocket in an early embryonic stage, that is to the amniotes with the exception of turtles. However the question is purely one of terminology, and need not be considered here.

Correlated with these two sensory areas, there was presumably at least a partial division of the olfactory nerve and bulb into two parts. Whether there was primitively a distinct accessory olfactory bulb cannot be told; if there was, modern urodeles have reduced the distinctness of this structure. The other possibility is that urodeles retain the primitive condition, and that the other groups have, phylogenetically, increased its independence from the main bulb.

The conditions found in the three orders of recent amphibians may easily be derived from such a hypothetical primitive form. In all three, the ventral sensory epithelium (or Jacobson's organ) has become restricted and is situated in a depression or pocket in the nasal wall. However there is no real resemblance between the pockets in the three groups, and no reason to assume that their formation did not occur independently in each group. In the Gymnophiona and Anura, but not in the Urodela, the accessory olfactory bulb is now a very distinct structure, as mentioned above.

In turtles the nasal anatomy also appears very primitive. As in all other amniotes, the accessory olfactory bulb is sharply defined, but the area covered by ventral sensory epithelium is extensive, more so than in any other living group. Although in sea turtles it has become restricted to small pockets, in most turtles the "Jacobson's organ" is merely the ventral half of the main nasal cavity. It appears probable that the latter condition is primitive; certainly there is no embryological evidence that turtle ancestors ever possessed a Jacobson's organ like that of the other amniotes. If they are primitive, then the evolutionary line culminating in turtles must have diverged from the main stream of reptilian evolution before the lines leading to the other modern reptilian groups, birds, and mammals had become distinct.

As was mentioned before, all other amniotes possess two major features in common: a definitive Jacobson's organ (at least in embryonic stages) and a concha. There is no convincing evidence for the existence of the latter structure in any lower group. After the acquisition of these two characters, the various groups diverged into three main lines. One, the reptilian subclass Lepidosauria, includes the Rhynchocephalia and the Squamata; here Jacobson's organ was retained and the nasal cavity remained relatively simple. Reptiles of the subclass Archosauria, crocodilians and the ancestors of birds (and presumably their fossil relatives including dinosaurs and others), lost Jacobson's organ completely, but evolved a postconcha. Subsequently different groups within this main line developed other specializations such as the preconcha of crocodiles. The third and last line is that of the mammal-like reptiles (Synapsida) and mammals. Their distinctive features have already been noted in the section on nasal anatomy. There were other phylogenetic lines of reptiles, but they are now extinct, and their nasal anatomy is unknown.

Such is a *possible* history of nasal evolution in tetrapods; naturally there are other possibilities, but the theory presented above seems, to me, best to explain

the features of nasal anatomy and embryology as they are known in modern forms. The most interesting and critical point is the isolated position of the order Chelonia, apparently not closely related to any other modern reptilian order. If the interpretation given above is not accepted, there are two other possibilities. First, the definitive Jacobson's organ and concha could be parallel developments in two or three of the other evolutionary lines; their very close embryological similarity in all groups (see fig. 3) renders this very unlikely, although it is possible, especially if it is assumed that the primitive reptiles possessed a hereditary tendency to form such structures. The other possibility is that turtle ancestors originally possessed both structures in question, but have completely lost them. Here again, there is no evidence for such a view. Jacobson's organ would not merely be lost; it would be lost as a separate organ, but its sensory epithelium would have had then to spread over the floor of the nasal cavity and assume a condition more like that found in urodeles than in any other group. Such a loss of the pit-like organ, coupled with a spread of the sensory epithelium, does not appear probable.

It is tempting to assume that the possession of a pocket containing the ventral sensory epithelium, that is a well defined Jacobson's organ, is primitive, since most groups do have such a pocket. However this could easily be a parallel development in several lines; in fact the great variation in the position of the pocket would seem to require it. Sea turtles have two pockets representing Jacobson's organ—they obviously have formed at least one independently. The frequency of the medial position, in most amniotes and anurans as opposed to urodeles and gymnophionans, may well indicate the primitive center of the ventral sensory area. In turtle embryos the ventromedial wall shows histological evidence of its sensory nature before the ventrolateral wall. However, there is no definite evidence for a ventromedial sensory pocket being a primitive tetrapod character.

Evidence from the Fossil Record

The only direct evidence of what has actually happened in evolution is that found in the fossil record; unfortunately there is almost no such evidence in the case of the nose. In no group of reptiles, extinct or living, is the nasal capsule ossified (Romer, 1956), and a cartilaginous capsule is not preserved in a fossil. However in some cases the surrounding bones do give some indications of the nasal anatomy.

Virtually nothing is known concerning the conchae of fossil forms. The advanced mammal-like reptiles (therapsids) almost certainly possessed a maxilloturbinal, a nasoturbinal, and a series of ethmoturbinals (Waston, 1913 and 1951); however the presence of an essentially mammalian condition in forms definitely ancestral to mammals and very distant from any other recent group is hardly surprising, and tells nothing about the origin of that condition. Camp (1930) has described ossified conchae in one fossil reptile, the phytosaur *Marchaeroprosopus*. The phytosaurs are an extinct group within the subclass Archosauria which superficially resemble crocodilians. Their nasal cavities were greatly modified for an aquatic life, with the external naris well posterior and dorsal on the snout. The conchae described by Camp lie anterior to both the external naris and the choana, and were apparently related to the septomaxilla; thus they do not appear to be readily comparable to any structure found in recent forms.

The only other fossil evidence worthy of note here concerns the olfactory nerves and bulbs. In some forms the anterior end of the braincase (the sphenethmoid) is ossified, and thus preserved in fossils; in such forms, the foramina for the olfactory nerve may be seen. Jarvik (1942) reports that, in all crossopterygians and in lungfish, there is

only a single foramen on either side, and hence no indication of any division of the olfactory nerve into medial and lateral trunks. However in the labyrinthodonts, among the most primitive of tetrapods, conditions vary. At least two forms, *Benthosuchus* (Bystrow and Efremov, 1940) and *Edops* (Romer and Edinger, 1942; Romer and Witter, 1942), resemble crossopterygians in the possession of a single foramen; however *Eryops* (Dempster, 1935; Sawin, 1941) has two or three foramina on each side. The medial one of these is sometimes thought to have transmitted a special medial branch of the olfactory nerve for the innervation of a Jacobson's organ. Various other labyrinthodonts lack an ossified sphenethmoid (Säve-Söderbergh, 1936; Wilson, 1941), and the situation in the group as a whole is not at all clear. Among the mammal-like reptiles, the primitive pelycosaurs possess a pair of foramina on either side (Romer and Price, 1940), but in a more advanced therapsid only one is present (*Ulemosaurus;* Efremov, 1940). The facts cited above do not appear to give any real assistance in understanding the nasal anatomy of the forms mentioned. A paired olfactory nerve foramen may indicate the presence of a Jacobson's organ or some similar structure, but it is, at best, a weak indication.

Synapsids, even the primitive pelycosaurs (Romer and Price, 1940), can be shown to have possessed olfactory lobes similar in gross form to those found in mammals. As in the case of the conchae found in therapsids and mentioned above, this merely confirms the long recognized fact that synapsids do resemble mammals in many ways.

Discussion

Finally, since the use of one character or one complex of characters can hardly be considered a safe basis for any phylogenetic conclusions, it is important to compare the conclusions reached after a study of nasal anatomy with the theories proposed by various workers on the basis of other structures. Naturally such a review must be very superficial due to the limitations of space; however the major theories of reptilian phylogeny can be considered briefly.

In the preceding sections of this paper, it has been assumed that the tetrapods are a monophyletic group, that is that terrestrial forms have arisen but once from crossopterygian ancestors. Although this is probably the most widely held view, several workers disagree. Säve-Söderbergh (1934), Jarvik (1942), and von Huene (1956) believe that there are two separate terrestrial lines; the Urodela and Gymnophiona are the living representatives of one, and the Anura and amniotes of the other. Jarvik bases his conclusions on a study of the snout in various recent forms and in the fossil crossopterygians. One group of the latter, the Porolepiformes, resembles closely the urodeles and another, the Osteolepiformes, the anurans. Among the characters which he cites is a ventromedian pocket for Jacobson's organ in osteolepiform, but not in porolepiform crossopterygians. Thus Jarvik homologizes the undoubted Jacobson's organ of most amniotes with the more questionable Jacobson's organ of frogs, but not with that of the other recent amphibians.

The anatomical data presented earlier do not give any strong evidence for or against such a theory. Certainly all terrestrial forms share certain characters, notably the presence of Bowman's glands and of two types of sensory olfactory epithelium with slightly separate neural connections (the latter may be secondarily lost as in crocodilians), which are not found in any *recent* fish. However no recent fish is closely related to the crossopterygian ancestors of tetrapods. *Latimeria,* the only surviving crossopterygian, is a member of the Coelacanthiformes, which, according to Jarvik, have a pattern of nasal anatomy very different from that of any other group. Thus it is quite possible that the hypothetical primitive

tetrapod condition described above applies equally to primitive crossopterygians. However Jarvik does not mention the turtles; if anurans and amniotes are considered to have an identical type of Jacobson's organ, then the chelonian nose presents a highly anomalous situation.

A more important problem is, therefore, the position of the turtles among the reptiles. In this discussion four lines of reptilian evolution must be considered; other lines which have no living descendants are not treated. First there are the turtles themselves. The remaining recent reptiles plus the birds fall into two major groups, the Lepidosauria (*Sphenodon,* lizards, and snakes) and the Archosauria (crocodilians and birds—the latter are not reptiles, but are descended from archosaurian ancestors). Both of the latter major lines are, primitively at least, characterized by the possession of two temporal fenestrae on each side of the skull, and are thus often grouped together as diapsids; although they are here treated as two lines, there is general agreement that they are more closely related to each other than to any other subdivision of the reptiles (see Romer, 1956, for a discussion of this point). Finally a fourth major phylogenetic line includes the Synapsida, or mammal-like reptiles, a group now extinct but including the ancestors of mammals.

The most primitive of fossil reptiles, and hence the presumed ancestors for all four lines mentioned above, are generally placed in the order Cotylosauria. However many recent authors, such as Olson (1947) and Watson (1957), consider this to be a rather artificial assemblage. It is therefore necessary to sudivide the cotylosaurs into two major groups, the diadectomorphs and the captorhinomorphs. Some authors recognize a third group of cotylosaurs, the seymouriamorphs; however others believe that these forms were amphibians or that they are to be included within the Diadectomorpha. Since there is general argreement that they are far more closely related to diadectomorphs than to captorhinomorphs, they may, for the purposes of this discussion, be included within the former group.

This gives a pattern of two primitive assemblages and four modern groups to be derived from them. Of these four, two may quickly be disposed of since the fossil evidence appears to be unequivocal. The turtles are almost universally believed to be descended from diadectomorph ancestors, and the synapsids, and hence mammals, from captorhinomorphs; Gregory (1946 and 1948), Olson (1947), von Huene (1956), Romer (1956), and Watson (1957) all appear to be in agreement on both of these points. There are, of course, differences of opinion as to the exact ancestral branch within the major groups, but they are of minor importance. However the origin of the two diapsid lines, the lepidosaurs and archosaurs, is far from clear, and the question is still debated in the literature. Since there are two main groups of primitive reptiles, there are two major theories which could and have been proposed for the origin of the diapsids; both must be considered here.

Since, in their nasal anatomy, the diapsid reptiles resemble mammals more closely than turtles, the theory of the evolution of the nose presented above would indicate a captorhinomorph ancestry for these groups, both lepidosaurs and archosaurs. Such a captorhinomorph ancestry has been most strongly advocated by Olson (1947); his conclusions are based on a study of the skulls, especially the temporal and basicranial regions, in primitive reptiles. Olson considers the differences between the groups of cotylosaurs so basic that he divides the Reptilia into two subclasses, the Parareptilia for the diadectomorphs and turtles, and the Eureptilia for the captorhinomorphs and their descendants, both diapsid and mammal-like reptiles (see fig. 4).

Other workers have apparently shared Olson's beliefs, although they have not given them formal taxonomic recognition. Thus Franz (1931) shows a diagram in

which the Chelonia are the first side-branch of the reptilian stock; the separation of diapsid and mammal-like reptiles is indicated to be a more recent occurrence. Gregory (1948) mentions, and apparently accepts, Olson's conclusions, although he does not consider the question in detail. Romer (1956) also seems to tend toward this view, although with reservations. He describes the skulls of the millerettids, a small group of reptiles from the Permian of South Africa, and states that they are possible ancestors for all the diapsid reptiles. They are also very similar to captorhinomorphs, except that the millerettids possess a shallow otic notch which is absent in members of the latter group. He concludes that they could either have arisen from captorhinomorphs by the development of an otic notch, or that they could have arisen from some form allied to the diadectomorphs in which an otic notch is consistently present; however the known diadectomorphs all show specializations which eliminate them as possible millerettid ancestors (Romer, 1956, pp. 104 and 105).

The second possible theory, that all diapsid reptiles arose from a diadectomorph (sensu lato) ancestor, has enjoyed a somewhat greater popularity. This theory is based on two main lines of evidence, one of them based on the soft parts of recent forms. Goodrich (1916) first called attention to the basic differences in the heart and aortic arches of all modern reptiles and birds as compared with mammals. He was unable to see any method by which one pattern could arise from the other, and therefore postulated that the common ancestors of the living amniotes must have possessed an essentially amphibian condition. Further elaborations of his argument occur in the works of Goodrich (1930) and von Hofsten (1941). On the basis of the differences in the heart and aortic arches, Goodrich divided the reptiles into three main groups: the Sauropsida, including turtles, lepidosaurs, archosaurs, and fossil relatives; the Theropsida, including mammal-like reptiles and relatives; and the Protosauria for the presumed common ancestors of the other two groups. He also believed that the nature of the fifth metatarsal could be used as a character separating sauropsids from theropsids, but more recent workers have denied this (Vaughn, 1955, and Watson, 1957).

FIG. 4

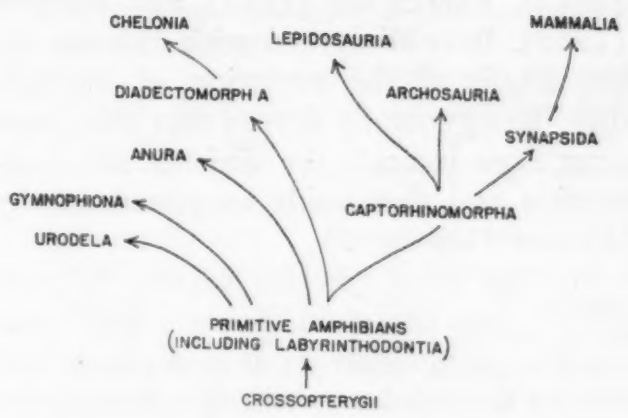

FIG. 5

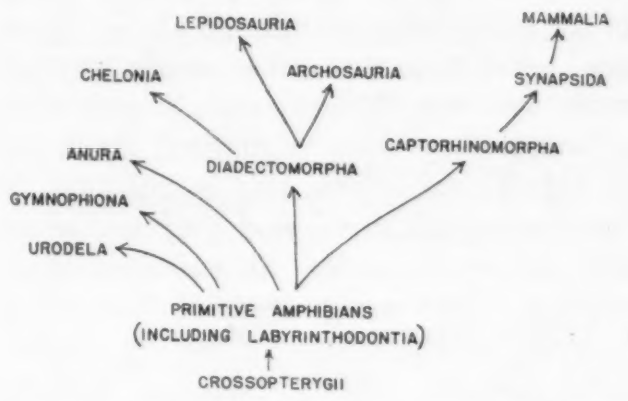

FIG. 4. Phylogenetic tree of the tetrapods according to the theories of Olson and others.
FIG. 5. Phylogenetic tree of the tetrapods according to the theories of Watson and others.

The possibility that the sauropsid-theropsid dichotomy might equal that between diadectomorphs and captorhinomorphs is immediately obvious, and has been championed by Watson (1951, 1953, 1954, and 1957). The main problem was that the heart characters cannot be seen in fossil forms and the metatarsal did not appear to be a reliable criterion; thus there was no way to distinguish fossil sauropsids from fossil theropsids. Watson proposed using the nature of the middle ear as such a distinguishing characteristic, and has elaborated on that idea in the papers cited above. Although

many other workers, such as Westoll (1943), Parrington (1949), and Vaughn (1955), have disagreed with Watson on the details of the evolution of the ear, they have generally agreed that this character does indicate the division into sauropsids and theropsids as postulated by Watson (see fig. 5).

In his most recent paper, Watson (1957) has proposed giving formal taxonomic recognition to this division and defines the subclasses Reptilia Sauropsida and Reptilia Theropsida. This paper is mainly concerned with a careful study of the millerettids mentioned above. Watson concludes that they merit ordinal rank (as the Millerosauria) and that, although they show a marked similarity to captorhinomorphs, this is due only to both being primitive, and they are properly to be regarded as primitive sauropsids. His assignment of the group is based on the nature of the ear region. Like Romer (1956), Watson believes that the millerettids are ancestral to the diapsid reptiles, both the lepidosaurs and the archosaurs.

These conclusions force Watson to postulate that the sauropsids arose from a stock which is very poorly known in the fossil record. The millerettids are one progressive line of this stock and the known diadectomorphs are very early and specialized branches of it. Thus the two primitive assemblages are, according to Watson, not just the diadectomorphs and captorhinomorphs, but the diadectomorphs plus millerettids plus unknown forms and the captorhinomorphs.

Conclusions

Thus it does not appear possible, at this time, to reach any definite conclusions on the early history of reptilian evolution. There is undoubtedly much real evidence for the division of all reptiles into sauropsids (including diadectomorphs) and theropsids (including captorhinomorphs). Goodrich's original evidence from the heart and aortic arches remains unchallenged, and the evidence from the ear, despite disagreement concerning the details, seems strong. However there are also some conflicting data, so the question is not absolutely settled. As noted by Olson and admitted by all workers, the known diadectomorphs do not seem to be available as ancestors for the diapsid reptiles; the turtles, however, do seem to be related to them. The nasal anatomy appears to confirm the isolated position of the turtles. Possibly (as admitted by Watson, 1957) the diadectomorphs are indeed not closely related to the other sauropsids, but form an entirely separate group. If that is the case, then reptiles would be divided into three main lines, and the relationships between them could only be considered obscure.

Only one definite conclusion seems justified—that more information is needed. The greatest need is, of course, for more information concerning the earliest reptiles; unfortunately this may never be available. However it is also possible that the study of more of the soft parts in recent animals may, upon analysis, shed some light on the early history of the reptiles. So far only three organs have been thus used, the heart and aortic arches, the ear, and the nose. Although such studies can probably never produce absolutely conclusive results, they may very well result in sufficient circumstantial evidence to make it possible to construct a highly probable phylogenetic tree of the reptiles.

Summary

The structure and development of the nasal cavities in recent forms appear to indicate that the turtles occupy a very isolated position in the phylogeny of amniotes. They lack completely the concha and typical Jacobson's organ found in other reptiles, birds, and mammals. These facts may be taken as evidence for the division of reptiles into the Parareptilia and Eureptilia, and against a split into Sauropsida and Theropsida. However until much more evidence is available, no definite conclusions on the merits of these two theories are possible.

Literature Cited

Bystrow, A. P., and J. A. Efremov. 1940. *Benthosuchus sushkini* Efr.—A labyrinthodont from the Eotriassic of Sharjenga River. Trav. Inst. Paleont., Acad. Sci. URSS, **10** (1) : 1–152.

Camp, C. L. 1930. A study of the phytosaurs with description of new material from western North America. Mem. Univ. California, Berkeley, **10**: x + 174 pp.

Crosby, E. C., and T. Humphrey. 1939. Studies of the vertebrate telencephalon. I. The nuclear configuration of the olfactory and accessory olfactory formations and of the nucleus olfactorius anterior of certain reptiles, birds, and mammals. J. Comp. Neurol., **71**: 121–213.

Dempster, W. T. 1935. The brain case and endocranial cast of *Eryops megacephalus* (Cope). J. Comp. Neurol., **62**: 171–196.

Efremov, J. A. 1940. *Ulemosaurus svijagensis* Riab.—Ein Dinocephale aus den Ablagerungen des Perm der UdSSR. Nova Acta Leopoldina, (N.F.), **9** (59) : 155–205.

Franz, V. 1931. Systematik und Phylogenie der Wirbeltiere. *In* Bolk, L., *et al.* (eds.). Handbuch der vergleichenden Anatomie der Wirbeltiere. Berlin and Vienna, Urban und Schwarzenberg. **1**: 185–268.

Goodrich, E. S. 1916. On the classification of the Reptilia. Proc. Roy. Soc. London, (B), **89**: 261–276.

——. 1930. Studies on the structure and development of vertebrates. London, Macmillan. xxx + 837 pp.

Gregory, W. K. 1946. Pareiasaurs versus placodonts as near ancestors to the turtles. Bull. Amer. Mus. Nat. Hist., **86** (6) : 275–326.

——. 1948. Evolution emerging. New York, Macmillan. 2 vols., xxvi + 1749 pp.

Herrick, C. J. 1921. The connections of the vomeronasal nerve, accessory olfactory bulb and amygdala in Amphibia. J. Comp. Neurol., **33**: 213–280.

von Hofsten, N. 1941. On the phylogeny of the Reptilia. Zool. Bidrag, **20**: 501–521.

von Huene, F. R. 1956. Paläontologie und Phylogenie der niederen Tetrapoden. Jena, Gustav Fischer. xii + 716 pp.

Jarvik, E. 1942. On the structure of the snout of crossopterygians and lower gnathostomes in general. Zool. Bidrag, **21**: 235–675.

Matthes, E. 1934. Geruchsorgan. *In* Bolk, L., *et al.* (eds.). Handbuch der vergleichenden Anatomie der Wirbeltiere. Berlin and Vienna, Urban und Schwarzenberg. **2** (2) : 879–948.

Olson, E. C. 1947. The family Diadectidae and its bearing on the classification of reptiles. Fieldiana: Geol., **11** (1) : 1–53.

Parrington, F. R. 1949. Remarks on a theory of the evolution of the tetrapod middle ear. J. Laryngol. Otol., **63**: 580–595.

Parsons, T. S. In press. Studies on the comparative embryology of the reptilian nose. Bull. Mus. Comp. Zool. Harvard Coll.

Romer, A. S. 1956. Osteology of the reptiles. Chicago, Univ. Chicago Press. xxi + 772 pp.

Romer, A. S., and T. Edinger. 1942. Endocranial casts and brains of living and fossil Amphibia. J. Comp. Neurol., **77**: 355–389.

——, and L. I. Price. 1940. Review of the Pelycosauria. Geol. Soc. Amer. Special Paper 28. x + 538 pp.

——, and R. V. Witter. 1942. *Edops,* a primitive rhachitomous amphibian from the Texas red beds. J. Geol., **50**: 925–960.

Säve-Söderbergh, G. 1934. Some points of view concerning the evolution of the vertebrates and the classification of this group. Ark. Zool., **26A** (17) : 1–20.

——. 1936. On the morphology of Triassic stegocephalians from Spitsbergen, and the interpretation of the endocranium in the Labyrinthodontia. Kungl. Svenska Vetenskapsakad. Handl., (3), **16** (1) : 1–181.

Sawin, H. J. 1941. The cranial anatomy of *Eryops megacephalus.* Bull. Mus. Comp. Zool. Harvard Coll., **88** (5) : 407–463.

Vaughn, P. P. 1955. The Permian reptile *Araeoscelis* restudied. Bull. Mus. Comp. Zool. Harvard Coll., **113** (5) : 303–467.

Watson, D. M. S. 1913. Further notes on the skull, brain, and organs of special sense in *Diademodon.* Ann. Mag. Nat. Hist., (8), **12**: 217–228.

——. 1951. Paleontology and modern biology. New Haven, Yale Univ. Press. xii + 216 pp.

——. 1953. The evolution of the mammalian ear. Evolution, **7**: 159–177.

——. 1954. On *Bolosaurus* and the origin and classification of reptiles. Bull. Mus. Comp. Zool. Harvard Coll., **111** (9) : 295–449.

——. 1957. On *Millerosaurus* and the early history of the sauropsid reptiles. Phil. Trans. Roy. Soc. London, (B), **240** (673) : 325–400.

Westoll, T. S. 1943. The hyomandibular of *Eusthenopteron* and the tetrapod middle ear. Proc. Roy. Soc. London, (B), **131**: 393–414.

Wilson, J. A. 1941. An interpretation of the skull of *Buettneria,* with special reference to the cartilages and soft parts. Contrib. Mus. Paleont. Univ. Mich., **6** (5) : 71–111.

Zuckerkandl, E. 1910. Ueber die Wechselbeziehung in der Ausbildung des Jacobsonschen Organs und des Riechlappens nebst Bemerkungen über das Jacobsonsche Organ der Amphibien. Anat. Hefte, Abt. I, **41**: 1–75.

CHROMOSOMAL EVOLUTION IN THE SUBTRIBE ASTERINAE

YUKIO HUZIWARA

Biological Institute, Kobe University, Mikage, Kobe, Japan

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A considerable number of species belonging to five genera of the subtribe Asterinae, namely, *Aster* L., *Gymnaster* Kitamura, *Kalimeris* Cass., *Heteropappus* Less. and *Erigeron* L., are found growing in the wild in Japan (Kitamura, 1937). Three of these genera, *Gymnaster, Kalimeris* and *Heteropappus,* are endemic to East Asia, while the remaining two genera, *Aster* and *Erigeron,* are of widespread occurrence, being found in North America and in Asia. In the Asterinae chromosomal studies seemed to have been greatly neglected, and therefore this subtribe has proven a most fertile field for investigation. As has partly been shown in the previous papers of the writer (Huziwara, 1950, 1953, 1954a, 1954b, 1955a, 1955b, 1955c, 1956, 1957a, 1957b, 1957c, 1958a, 1958b), these wild races, taken together with their cultivated relatives, form a very interesting problem for phylogenetic studies. This is a summarized review of the karyotype studies in the Asterinae.

For our early knowledge concerning the cytology of the subtribe we are indebted to the pioneer work of Tahara and Shimotomai (1926). From their studies of chromosome numbers of different species they clearly established a polyploid series of $n = 9$, 18 and 27. Subsequently, the following chromosome numbers, each representing a different polyploid level, have been found in the Asterinae: $2n = 10$, 16, 18, 20, 27, 32, 36, 48, 54, 63, 72 and 144. The numbers of taxa in each polyploid level of the Asterinae as determined from the previous studies of the writer and from those of other investigators are given in table 1. The polyploid index devised by Blackburn and Morton (1957) in an analysis of the incidence of polyploidy in the Caryophylaceae is also presented in this table. The index clearly shows the highly polyploid nature of the subtribe Asterinae.

The wide range in chromosome numbers is very noticeable, varying from a complement as high as $2n = 144$ to as few as $2n = 10$. As might be expected, the majority of the plants are either diploids or tetraploids and have chromosome numbers of $2n = 18$ and $2n = 36$, respectively. The tri-, hexa-, hepta-, octo- and 16-ploid forms are more rare. Out of the 129 euploid races reported, 70 diploids (54 per cent), 5 triploids, 34 tetraploids (26 per cent), 12 hexaploids, 2 heptaploids, 5 octoploids and 1 16-ploid are found. In addition to the euploids, hyperpolyploid ($2n = 38$, 49) as well as hypopolyploid races ($2n = 46$, 52, 68) were encountered. It is significant that the majority of the complements are multiples of nine. Consequently, the primitive basic chromosome number for the subtribe Asterinae is considered to be nine. And it is from this base number that the polyploids are largely derived. In *Aster,* diploid, tetraploid, hexaploid and octoploid chromosome numbers occur. In *Gymnaster,* diploid, triploid, tetraploid and 16-ploid, in *Kalimeris,* diploid, hexaploid, heptaploid and octoploid, and in *Erigeron,* diploid, triploid, tetraploid, hexaploid and heptaploid chromosome numbers are found. In *Heteropappus* only the tetraploid chromosome number is known. Except for three races of *Aster ageratoides* Turcz., namely, subspecies *leiophyllus* (Fr. et Sav.) Kitamura, its variety *tenuifolius* Kitamura and subspecies *amplexifolius* (Sieb. et Zucc.) Kitamura, which

TABLE 1. *Numbers of taxa in each polyploid level of the Asterinae*

Genus	Basic number	Euploids							Aneuploids					Polyploid index*
		2x	3x	4x	6x	7x	8x	16x	2x+1	4x+2	6x−2	6x+1	8x−4	
Aster	b=9	39	2	24	6	—	2	—	2	2	1	—	—	3.21
Aster	b=8	3	—	1	2	—	2	—	—	—	1	1	—	5.00
Aster	b=5	6	—	2	—	—	—	—	—	—	—	—	—	2.50
Gymnaster	x=9	3	2	1	—	—	—	1	—	—	—	—	—	4.57
Kalimeris	x=9	4	—	—	1	1	1	—	—	—	—	—	1	4.63
Heteropappus	x=9	—	—	3	—	—	—	—	—	—	—	—	—	4.00
Erigeron	x=9	15	1	3	3	1	—	—	—	—	—	—	—	3.04
Totals		70	5	34	12	2	5	1	2	2	2	1	1	

* The polyploid index was prepared by dividing the sum of the indices of the polyploid levels by the number of taxa concerned.

have a diploid number of 18 and a race of subspecies *leiophyllus* with 54 chromosomes, all the subspecies and the varieties of *Aster ageratoides* (fig. 4) have a tetraploid number of 36 (Huziwara, 1957c). Asiatic species of *Aster* (figs. 1, 2, 3, 4) all have a basic number of nine, whereas the American species of *Aster* (figs. 11, 12, 13, 14) have three basic numbers, namely, five, eight and nine (Huziwara, 1958b). The lower basic numbers of five and eight are considered to be derived from nine by a gradual process of reduction. Judging from the number of taxa which have so far been determined as polyploids in the different species of the subtribe Asterinae, the role of polyploidy in the differentiation of the races is obvious. Although the origin of new and stable forms of plant species by means of hybridization supplemented by chromosome doubling is well known to cytogeneticists, the occurrence of autopolyploids in the wild is a rare phenomenon. Therefore, autopolyploidy as found in *Gymnaster savatieri* Kitamura (fig. 6) is of remarkable importance (Huziwara, 1954b).

The evolutionary trends of the karyotype in the Asterinae have been from chromosomes with median to subterminal centromeres, from large to small chromosomes, and from symmetrical to asymmetrical karyotypes. Similar trends are also amply demonstrated in the tribe Cichorieae (Stebbins, Jenkins and Walters, 1953).

The size of the chromosomes within the Asterinae varies to a very considerable degree. The absolute length of the chromosomes ranges from approximately 2μ to 12μ. Most of the members of Asterinae are characterized by having comparatively large chromosomes and do not show much difference in size within their complements. Typical complements are well exemplified in the sections Teretiachenium and Tripolium (fig. 3). Certain races included within the section Euaster, however, do show to some extent a difference in size of the chromosomes within the complement. The best example is *Aster ageratoides* subsp. *ovatus* var. *humilis* Nakai (fig. 4). In this variety the largest chromosomes of the complements are about six times as long as the smallest ones. Members of the genus *Erigeron* (figs. 8, 9) are also characterized by extremely short chromosomes. *Aster dubius* Onno ex Kitamura (fig. 5) which belongs to the section Alpigenia has sometimes been placed in the genus *Erigeron* (Ohwi, 1953). The similarity in karyotypes between *Aster dubius* and species of *Erigeron* suggested that this species rightly belonged to the genus *Erigeron* (Huziwara, 1957b).

Different types of chromosome morphology have been noted in different genera and the karyotypes have been found to

TABLE 2. *Data on somatic chromosomes in Asterinae*

Genus	Number of taxa investigated	Average chromosome length in μ	Average TF%*
Asiatic *Aster*	33	5.7	43
New World *Aster*	15	3.0	33
Gymnaster	4	5.5	42
Kalimeris	5	4.5	43
Heteropappus	3	4.2	42
Erigeron	11	3.0	34

* TF per cent represents the ratio in percentage of the total sum of short arm-lengths to the total sum of chromosome lengths.

vary considerably from species to species. Thus the heterogeneity of the subtribe has been clearly demonstrated. Among the species examined cytologically some are morphologically highly-varying and have been divided into a number of races and varieties, as in the case of *Aster ageratoides,* while others vary to a much lesser degree.

As regards the symmetry of karyotypes (Stebbins, 1950), symmetrical karyotypes are found in seven sections, namely, Euaster (figs. 1, 2, 4), Teretiachenium, Pseudocalimeris, Tripolium (fig. 3), Homolepis (fig. 6), Asteromoea (fig. 7) and Cordifolium and the genus *Heteropappus* (fig. 10). Members of the genus *Erigeron* (figs. 8, 9) and the North American species of *Aster* (figs. 11, 12, 13, 14) are representative of a more asymmetrical karyotype. These differences can be clearly shown by the average TF per cent in table 2. TF per cent represents the ratio in percentage of the total sum of short arm-lengths to the total sum of chromosome lengths. In plants with all the chromosomes medially attached TF per cent attains to fifty per cent, whereas in plants with all the chromosomes terminally attached TF per cent is reduced to zero. In strong contrast to the large symmetrical chromosomes of Asiatic asters (figs. 1, 2, 3, 4), the American taxa (figs. 11, 12, 13, 14) have small, asymmetrical chromosomes. This is an indication that the subtribe Asterinae has evolved much further on the American continent.

It is an interesting fact that sections of Asiatic *Aster* have karyotypes quite characteristic of themselves, and that their constituent species show marked similarity in their chromosome morphology (Huziwara, 1957b). However, difference in chromosome morphology as well as in external characters between the *leiophyllus* and *ovatus* groups within *Aster ageratoides* was found (Huziwara, 1957c). Since the two varieties of *Aster dimorphophyllus* Fr. et Sav., namely, *indivisus* Makino and *divisus* Makino, agree in the details of their chromosome structure as far as can be detected, it would seem that variation between them has been brought about through gene mutation (Huziwara, 1957b). There are some other differences. Kitamura's two sections of the genus *Gymnaster,* namely, Homolepis (fig. 6) and Crassifolium, are characterized by differences in karyotype (Huziwara, 1954b). The section Crassifolium has strikingly smaller chromosomes than the section Homolepis from which it is probably derived. The two sections of the genus *Kalimeris,* namely, Asteromoea (fig. 7) and Cordifolium, are also characterized by differences in karyotype as well as by various well-marked morphological features (Huziwara, 1955b).

The repeated occurrence of similar types of chromosomes in the complement of the polyploid species indicates that duplication of some of the members of the ancestral set has taken place and evidently the plant appears to be a secondarily balanced polyploid. Some species of *Aster* with a high number of chromosomes, such as *Aster tataricus* L. with fifty-four, possess chromosomes which show a marked similarity to the chromosomes of diploids such as *Aster maackii* Regel (fig. 1) and *Aster fastigiatus* Fischer (fig. 2). This leads one to assume that the members with a high num-

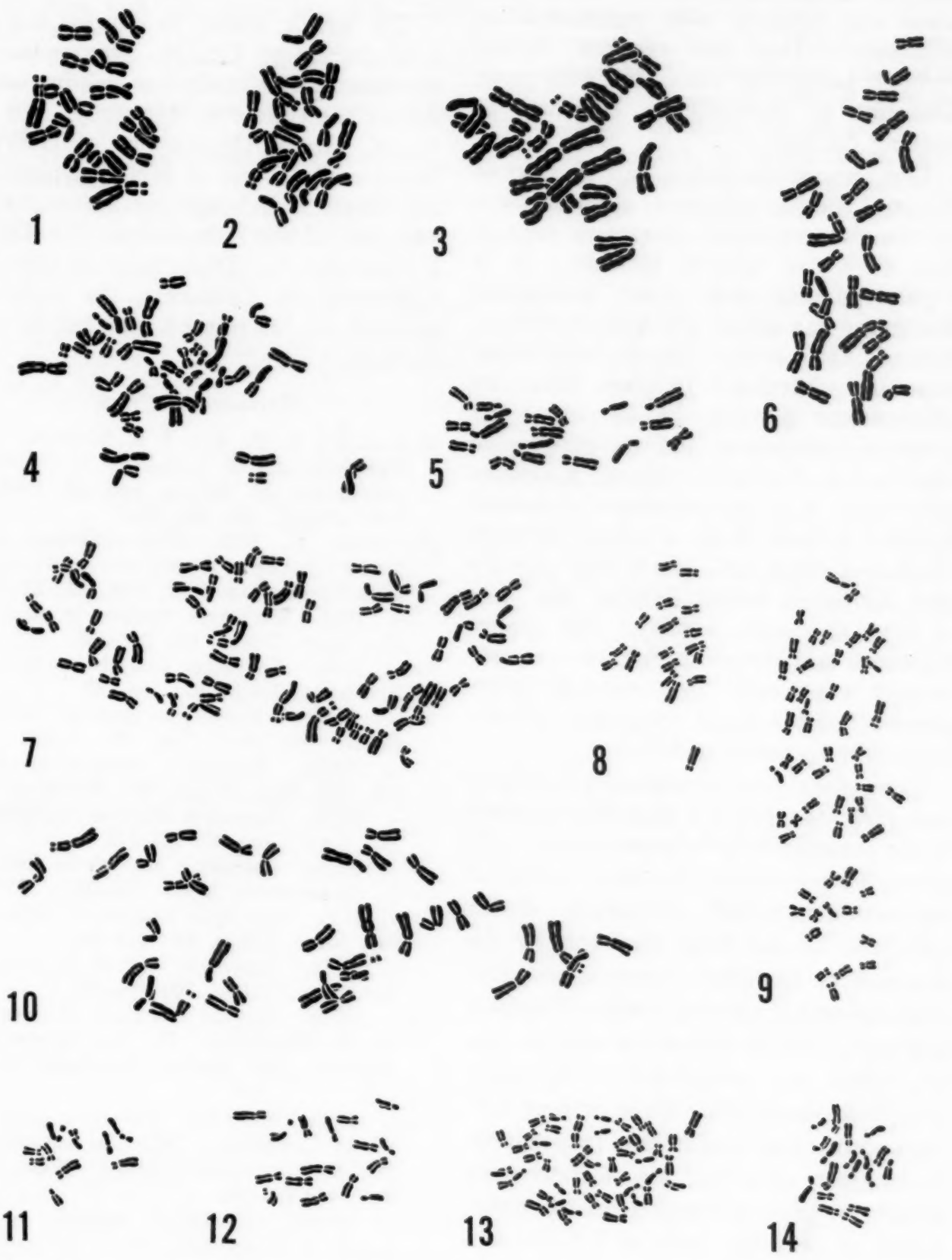

PLATE 1. Somatic chromosomes of the subtribe Asterinae. 1–10. Asiatic species: 1. *Aster maackii*, $2n = 18$; 2. *A. fastigiatus*, $2n = 18$; 3. *A. tripolium*, $2n = 18$; 4. *A. ageratoides* subsp. *ovatus* var. *humilis*, $2n = 36$; 5. *A. dubius* subsp. *glabratus* (*Erigeron thunbergii* var. *glabratus*), $2n = 18$; 6. *Gymnaster savatieri* $3x$, $2n = 27$; 7. *Kalimeris incisa*, $2n = 72$; 8. *Erigeron acre*, $2n = 18$; 9. *E. flahaultianum*, $2n = 54$; 10. *Heteropappus leptocladus*, $2n = 36$; 11–14. New World species: 11. *Aster exilis*, $2n = 10$; 12. *A. occidentalis*, $2n = 16$; 13. *A. novi-belgii*, $2n = 48$; 14. *A. modestus*, $2n = 18$. × 1200.

ber of chromosomes are derivatives of some wild ancestor with eighteen chromosomes. This has resulted mainly through polyploidy associated with some alteration in chromosome structure to varying degrees.

One sees various individuals of *Aster* of doubtful specific reference; some of them by their intermediate characters suggest that they are natural hybrids. It is highly possible that *Aster hashimotoi* Kitamura has arisen through hybridization of *Aster scaber* Thunb. with *Aster rugulosus* Maxim. Judging from its chromosome number, its karyotype, its external appearance and its geographic distribution, *Kalimeris yomena* Kitamura ($2n = 63$) is to be considered a natural hybrid derived from a cross between *Kalimeris incisa* DC. ($2n = 72$) (fig. 7) and *Kalimeris indica* Schultz Bip. ($2n = 54$) (Huziwara, 1955b). The genera *Kalimeris* and *Heteropappus* are so closely related genetically that natural intergeneric hybrids occur frequently (Huziwara, 1950; Inoue, 1955).

The genera *Aster, Gymnaster, Kalimeris* and *Heteropappus* are also characterized by the presence of L^{2E}-chromosomes. L^{2E}-chromosomes denote the large nucleolar chromosomes which are clearly distinguishable by the large size and by the presence of secondary constriction (Shimotomai and Huziwara, 1942). Triploids and tetraploids of *Gymnaster* species (fig. 6), which are considered to be autopolyploids, have either three or four L^{2E}-chromosomes of similar size, respectively. In contrast, allopolyploids of *Aster* have either two pairs of unequal sized chromosomes or only one pair of L^{2E}-chromosomes (fig. 4). It is generally believed that an allopolyploid species should become progressively diploidized until chromosome behavior resembles that of the normal diploid species (Stebbins, 1947). Such a trend seems possible in the alteration of the somatic as well as the meiotic chromosomes in the Asterinae.

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Literature Cited

Blackburn, K. B., and J. K. Morton. 1957. The incidence of polyploidy in the Caryophyllaceae of Britain and of Portugal. New Phytol., **56**: 344–351.

Huziwara, Y. 1950. *Heterokalimeris maruyamae* Kitamura: A new intergeneric hybrid of Astereae. Jap. Jour. Gen., **25**: 25–26.

——. 1953. Karyotype analysis in *Aster*. I. Bot. Mag., Tokyo, **66**: 262–268.

——. 1954a. Karyotype analysis in *Aster*. II. Bot. Mag., Tokyo, **67**: 184–189.

——. 1954b. Karyotype analysis in *Gymnaster*. Jap. Jour. Gen., **29**: 76–82.

——. 1955a. Karyotype analysis in *Aster*. III. Bot. Mag., Tokyo, **68**: 98–102.

——. 1955b. Karyotype analysis in *Kalimeris*. Jap. Jour. Gen., **30**: 118–123.

——. 1955c. Karyotype analysis in *Erigeron*. La Kromosomo, **25–26**: 923–928.

——. 1956. Karyotype analysis in *Aster*. IV. Bot. Mag., Tokyo, **69**: 119–124.

——. 1957a. Karyotype analysis in *Aster*. V. Bot. Mag., Tokyo, **70**: 198–201.

——. 1957b. Karyotype analysis in some genera of Compositae. II. The karyotype of Japanese *Aster* species. Cytologia, **22**: 96–112.

——. 1957c. Karyotype analysis in some genera of Compositae. III. The karyotype of the *Aster ageratoides* group. Amer. Jour. Bot., **44**: 783–790.

——. 1958a. Karyotype analysis in some genera of Compositae. IV. The karyotype within genera *Gymnaster, Kalimeris* and *Heteropappus*. Cytologia, (In press).

——. 1958b. Karyotype analysis in some genera of Compositae. V. The karyotype of American *Aster* species. Jap. Jour. Gen., (In press).

Inoue, S. 1955. Cytological studies on the natural hybrid arose from the genus *Kalimeris* and *Heteropappus*. Jap. Jour. Gen., **30**: 169.

KITAMURA, S. 1937. Compositae Japonicae. I. Mem. Coll. Sci. Kyoto Imp. Univ. Ser. B, **13**: 1–421.

OHWI, J. 1953. Flora of Japan. Tokyo.

STEBBINS, G. L. 1947. Types of polyploids: their classification and significance. Adv. Gen., **1**: 403–427.

——. 1950. Variation and evolution in plants. New York.

——, J. A. JENKINS AND M. S. WALTERS. 1953. Chromosome and phylogeny in the Compositae, tribe Cichorieae. Univ. Calif. Publ. Bot., **26**: 401–430.

SHIMOTOMAI, N., AND Y. HUZIWARA. 1942. Zytologische Untersuchungen über *Aster, Gymnaster, Kalimeris* und *Heteropappus* aus Japan. Cytologia, **12**: 206–218.

TAHARA, M., AND N. SHIMOTOMAI. 1926. Chromosompolyploidie bei *Aster* und dessen verwandten Gattungen. Bot. Mag., Tokyo, **40**: 132–136.

PREADAPTATION AND MULTIPLE EVOLUTIONARY PATHWAYS[1]

WALTER J. BOCK

Biological Laboratories, Harvard University, Cambridge 38, Massachusetts

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INTRODUCTION

The origin of radically new structures has always been one of the most fascinating—and one of the most puzzling—aspects of the study of evolution. Even today, when the broad outlines of speciation and of modification in existing structures has been well established, understanding of the factors involved in the appearance of radically new structures (and with them, new taxonomic groups) is, at best, confused. Many of the unsolved problems of macroevolution[2] stem, I believe, from a failure to appreciate the full implications of two evolutionary principles—*preadaptation* and *multiple pathways of evolution.* I wish in this paper to discuss these concepts in the hopes of at least partly clarifying their operational mechanism and their significance in macroevolution. Although I place great importance on these concepts, I must emphasize that I do not believe that they provide the solution to all the problems of macroevolution. Furthermore, I am aware that I omit many important phases of macroevolution, but I have purposely limited this paper to a discussion of preadaptation and of multiple pathways of evolution. For a discussion of all aspects of macroevolution, the reader is referred to Simpson's "The major features of evolution." I wish at this time to acknowledge my debt to this book. It has served as the basis for this paper and although I may differ from it in some points, these differences are usually differences in emphasis and statement, not in basic ideas. This paper grew out of a study of the avian basitemporal articulation—a secondary articulation of the mandible—which supplies most of my examples. I shall also include some discussion of the mammalian jaw articulation (even though it is a side issue) because of the almost perfect analogy between its evolution and that of the basitemporal articulation, and because it supplies additional examples of preadaptation.

THE BASITEMPORAL ARTICULATION

Structure: The basitemporal articulation is present in many groups of birds and well developed in some, yet for some reason it has escaped the attention of ornithologists and anatomists. It has been described only once before, by Shufeldt in the 1890's for the skimmer, gulls and terns, but this description has been so completely overlooked that the basitemporal articulation may be regarded as an essentially unknown structure. A full description of its structure, function and occurrence will be presented elsewhere (Bock, ms.); only a brief summary is given here. Most of the necessary evidence supporting the statements on the function, evolution and so forth of the basitemporal articulation have been omitted from the present paper; these can be found in the above cited paper.

The highly developed basitemporal articulation of the skimmer, *Rynchops nigre* (fig. 1), may serve as the basis for description. In this species, the medial process of the mandible ex-

[1] Dedicated to Erwin Stresemann on the occasion of his 70th birthday in admiration and appreciation of his contribution to the fields of ornithology and evolution.

[2] To me, camroevolution implies an evolutionary change at least on the generic or familial levels. It must be a change larger than minor changes in color, size, proportions and so forth which would be microevolutionary changes (see, also, Simpson, 1953, pp. 338–340). Macroevolution is a vague term, not differing sharply from microevolution, and is used only to emphasize a "larger" evolutionary change, not a different type of evolutionary change. I would include Simpson's megaevolution in macroevolution, but this is only a matter of taste.

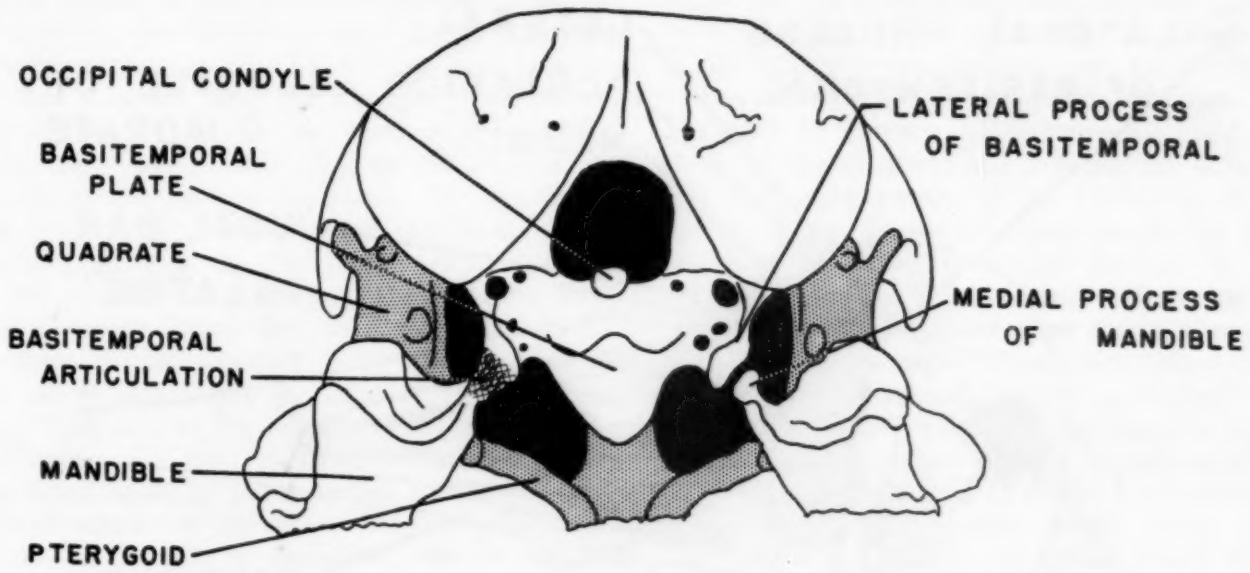

FIG. 1. Skull of a skimmer seen from the postero-ventral side. The basitemporal articulation is shown on the left side of the skull (cross-hatching), but has been removed on the right side to show the processes of the medial brace. The deep-lying bones are stippled for contrast.

tends upwards toward the basitemporal plate and abuts against the elongated lateral process of that bone. Both the medial process of the mandible and the lateral process of the basitemporal plate bear an articular surface on their tip. Study of histological sections of the basitemporal articulation of the skimmer proved that it is a true diarthrosis,[3] but one with dense fibrocartilage, instead of hyaline cartilage, articular pads. In a species lacking the basitemporal articulation, such as the boat-tailed grackle, *Cassidix mexicanus* (fig. 2), the medial process of the mandible may approach the base of the skull, but a distinct gap separates the two bones. A weakly developed basitemporal articulation can be seen in the ringed plover, *Charadrius hiaticula* (fig. 3); in this bird, the medial process of the mandible abuts against the weakly developed lateral process of the basitemporal plate, but the articulation is an amphiarthrosis.

Function: The basitemporal articulation is part of a brace—the medial brace of the mandible—formed by the medial process of the mandible abutting against the basitemporal plate. Associated with many types of feeding in birds are strong forces that tend to push the lower jaw backwards or to the side. The articular-quadrate hinge of many birds does not provide sufficient support for the mandible when the bill is opened; hence the lower jaw could disarticulate when the bird is feeding if there were no additional support for the mandible. The medial brace supplies this needed support and thus functions to prevent the possible disarticulation of the quadrate hinge when there are excessive forces acting on the depressed mandible. For example, the skimmer feeds by flying low over the water and inserting its knife-like mandible into the water. When a fish (or an obstacle) hits the bill, the head is jerked violently downwards and backwards by the force of the collision. At the same instant, the bill is closed and the fish is caught. The force with which a skimmer hits a fish or an obstacle is sometimes great enough to break off the tip of the horny covering of the mandible. This force of collision is transmitted directly to the jaw suspension. The condyles of the articular-quadrate hinge in the skimmer are not arranged to withstand the violent backwards force that accompanies the catching of its prey; the mandible would disarticulate unless there were some additional means of support for it. Protection against such disarticulation is supplied by the highly developed medial brace.

Evolution: Study of the evolution of a structure must not cease with the establishment of correct sequences of the structural modifications. This is a necessary step, but it is as important or even more important to determine the ancestral structural form and the selection

[3] Diarthroses are the normal vertebrate articulations in which the articulating surfaces of the bones are covered with cartilage, the bones are separated by an articular cavity filled with fluid, and the whole structure is encased by a synovial membrane composed of collagenous fibers. Amphiarthroses are simple articulations in which the bones are held together by bands of collagenous fibers; they are considered to be, both morphologically and functionally, intermediate between sutures and diarthroses.

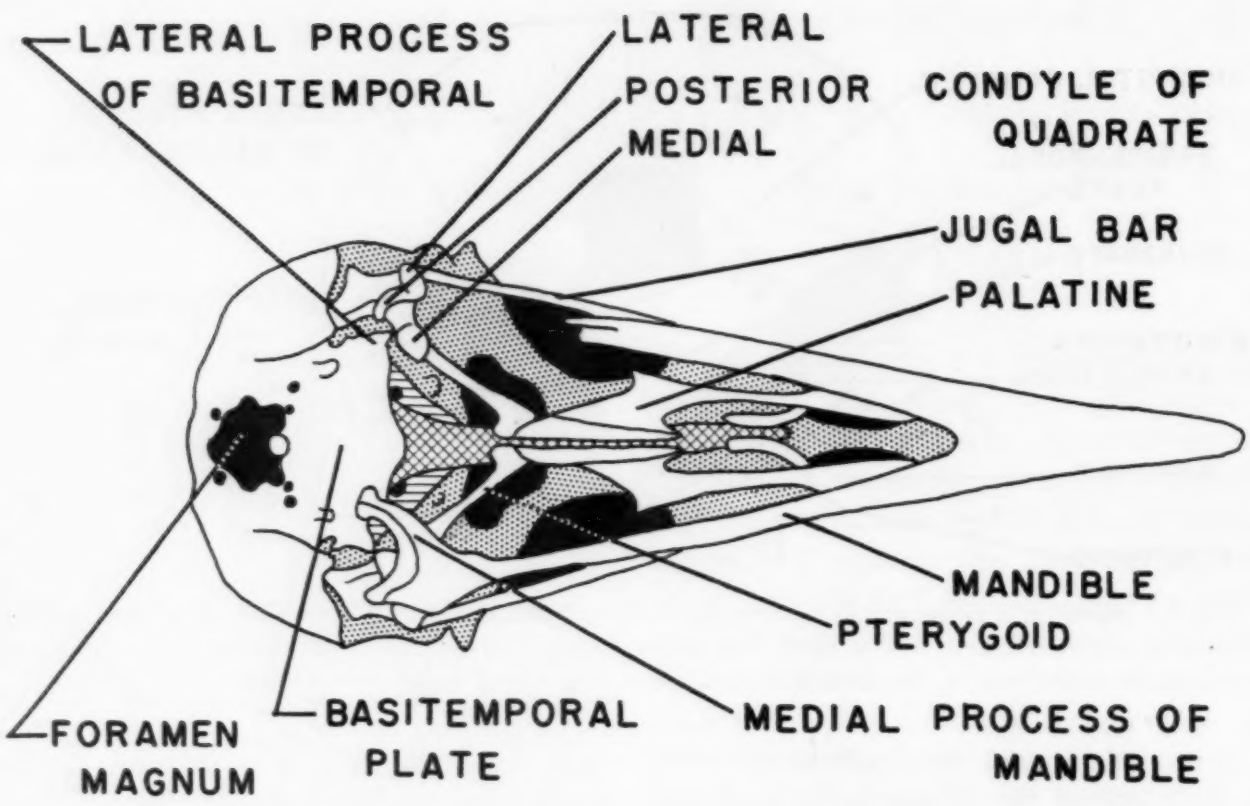

FIG. 2. Ventral view of the skull of a grackle. The posterior end of the right mandible was removed to expose the condyles of the quadrate. On the left side, the medial process of the mandible is seen approaching the base of the skull. The deep-lying bones are shaded for contrast.

forces [4] guiding the evolution of the structure. In discussions of the origin of a new structure, it is also necessary to know the "prehistory" of its several component parts.

The basitemporal articulation is part of the medial brace of the mandible, which is composed of the medial process of the mandible and a process of the basitemporal plate. The particular process of the basitemporal plate taking part in the medial brace is not the same in all groups of birds. This variation need not concern us at this point; I shall return to it in the discussion of multiple pathways. The primary function of the medial brace, and hence the selection force guiding its evolution, is to prevent the disarticulation of the lower jaw. Strong stresses on the mandible plus an inadequate arrangement of the articular condyles of the quadrate hinge have brought this selection force into being. Yet the evolution of the medial brace in the entire class of birds is not a simple picture of such a structure developing every time need for it arose. Some families lack the brace when it would be expected from their feeding habits. Possibly in some cases, the brace was present, but was not detected in my survey of the occurrence of the medial brace in birds. Moreover, there are several ways to counteract strong forces on the quadrate hinge. In some families, the condyles of the quadrate hinge are completely adequate to withstand the disrupting forces; in others, the jaw muscles and ligaments inserting on the mandible may be sufficient to protect the quadrate hinge. A discussion of these other methods of preventing the disarticulation of the mandible would lead us too far from the central problems of this paper, hence I shall quite arbitrarily accept the development of the medial brace as the only adaptive response to the selection force for additional support of the mandible.

Evolution of the medial brace begins when a bird "acquires" a more "active" method of feeding. A more active method of feeding would increase the stress on the quadrate hinge —consequently, the appearance of a selection force for support of the mandible—and would also necessitate an increase in the action (strength) of the bill. Thus an associated, but almost completely independent, selection force for stronger jaw muscles will appear either previously to or simultaneously with the selection force for a brace of the mandible. With an increase in the strength of the jaw muscles, there must be a corresponding increase in the

[4] A selection force is defined as the selection for one particular trait in an organism. It is used to distinguish between the multitude of different selective demands on an organism. I personally prefer "selection force" over "selective force"; it is not necessary to use an adjective when forming a compound noun. Selection force is synonymous with selection pressure.

areas of origin and insertion for these muscles. Therefore, the medial process of the mandible would increase in length and breadth in response to this selection force for stronger jaw muscles. Consequently, as can be seen in the grackle and many other birds, the medial process approaches the base of the skull; this can safely be regarded as the primitive condition. With further increase in the length of the medial process—still in response to the selection force for greater muscular strength—the medial process would become long enough that it would at last touch the base of the skull and rub against it as the bill opens and closes. The structures are now in position—preadapted—to be acted upon by the selection forces for additional support of the mandible. The preadapted stage is difficult to recognize, but it may be present in the herons, especially the night-herons (*Nycticorax*), and the cuckoos. At this stage in the evolution of the medial brace, the sole requirement is that the bones be in contact with one another *only when the bill is opened.* Whether the medial process of the mandible loses contact with the base of the skull when the bill is closed is of no importance, since the selection force for additional support of the mandible operates only when the bill is opened. The evolved adaptation—the medial brace of the mandible—is simple and little changed, if any, from the preadapted condition; the medial process of the mandible merely presses against the base of the skull, thereby becoming a brace and in this way preventing any further opening or other movements of the mandible. But whenever two bones press against one another, some sort of articulation *must* develop. Thus an articulation will develop between the bones of the medial brace, perhaps only consisting of ligaments binding the two bones together—the condition in plovers. However, we must not think of the basitemporal articulation developing only as a result of the evolution of the medial brace; it may be present in the preadapted stage if the medial process of the mandible is in contact with the basitemporal plate. Hence it is incorrect to equate the presence of a basitemporal articulation with a functional medial brace unless other specialized features of the brace (e.g., fibrocartilage articular pads) are also present. With increasing stress on the mandible, there would be a stronger selection force acting on the simple brace. The final result would be a permanent brace of the mandible with the bones remaining in contact with one another at all times. Since the bones are permanently in contact with one another and since the contact must be firm but still movable, the basitemporal articulation would become a fully developed diarthrosis. This last stage is illustrated by the skimmer. Increase in the length of the medial process of the mandible has occurred many separate times during the evolution of birds; hence it can be concluded that the bracing of the mandible by its medial process and, with it, the development of the basitemporal articulation, has evolved independently several times, possibly as many as 15 times. At the same time, if the medial process of the mandible does not become long enough to touch the base of the skull, a medial brace could never evolve regardless of the strength

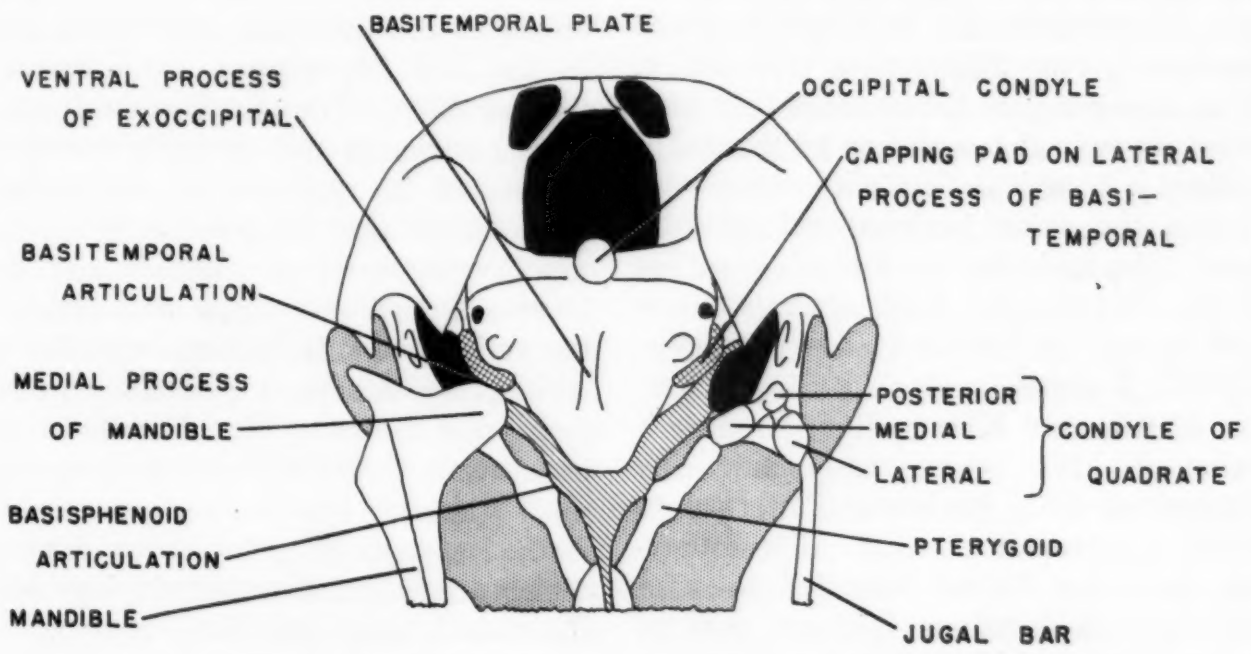

FIG. 3. Skull of a ringed plover seen from the postero-ventral side. The posterior part of the right mandible was removed to expose the quadrate. The cross-hatching indicates a pad of collagenous fibers on the lateral process of the basitemporal plate. The medial process of the mandible articulates against this pad. Again, the deep-lying bones are shaded for contrast.

of the selection force for additional support of the mandible.

The development of an amphiarthrosis and the change from an amphiarthrosis to a diarthrosis are relatively simple—and rapid—modifications, since the only requirement for the development of an articulation (in a phenotypic sense) is for two bones to rub against one another. A diarthrosis as found in the skimmer does not necessarily have to pass through an amphiarthrosis stage, but may arise directly when two bones come into contact. Diarthroses may develop during the life of an individual as in the case of an articulation developing where a fracture in a long bone failed to heal (Murray, 1937, p. 86) or in the examples of secondary articulations (op. cit., pp. 81–97). However, the normal embryological development of vertebrate articulations is apparently under direct genetical control (Murray, 1937) and not primarily under mechanical influences.

Comparison of the Avian Basitemporal Articulation and the Mammalian Jaw Articulation

One of the most interesting aspects of the avian basitemporal articulation is that it provides an analogy to the evolution of the mammalian jaw articulation. Here we have definite proof that a vertebrate can simultaneously have two separate articulations of the mandible—a clear contradiction of the common assumption that a vertebrate can have only a single functional jaw articulation. However, let us also compare the changes that have taken place in the evolution of the mammalian jaw articulation with the evolution of the avian basitemporal articulation. The basis for the following outline of the evolution of the mammalian jaw articulation is taken from Watson (1953), Kuhn-Schnyder (1954), Patterson (1956) and Kühne (1956). In addition, I have been greatly aided by discussions with Professor Patterson to whom I am most grateful. The following discussion is not intended to offer any new explanations for any part of mammalian evolution, but to point out the similarities between the evolution of the avian basitemporal articulation and what is already known or may be postulated for the evolution of the mammalian jaw articulation.

A shift in feeding habits apparently occurred in several different lines of therapsid reptiles at about the same time. Kuhn-Schnyder (1954, pp. 175–186) suggests that this shift was associated with the differentiation of the teeth and the accompanied need for a more efficient "bite." A delicate control of the jaw movements is needed for chewing with complex teeth, which is characteristic of the mammals. Whichever came first, the differentiated teeth or the more efficient control of the jaw movements, does not matter for this discussion; the important fact is that the temporal muscles increased in importance during the evolution of the therapsid reptiles. This change in the action of the jaw affected the entire muscle-bone system of the brain case and the mandible and led to a series of adaptations in these structures. Most important was the evolution in several lines of therapsid reptiles of a large process on the dorso-lateral side of the dentary (Watson, 1953, p. 169). This process corresponds to the coronoid process of the mammals and serves for the attachment of the temporal muscles. The coronoid process would become larger as the temporal muscles increased in size and importance as adductors of the mandible. Thus the coronoid process grew backwards and upwards toward the squamosal in response to the selection force for stronger temporal muscles. This new arrangement of muscles and bony levers of the jaw apparently rendered the articular-quadrate hinge a rather unsatisfactory, although still adaquate suspension of the mandible. Finally in some lines, the coronoid process grew upwards until it abutted against the squamosal and formed a supporting brace for the mandible, an articulation developing where the two bones came into contact. As pointed out above, development of an articulation is rapid once the bones are in contact. The mammal-like reptiles now had two separate pairs of jaw articula-

tions, thus reaching the intermediate stage in the evolution of the mammalian jaw articulation postulated by many authors and found recently by Crompton (1958) in *Diarthrognathus*. The most important functional problem lies in the arrangement of the hinges. A structure can have two or more pairs of hinges and still swing on them if they are aligned along the same axis such as the hinges of a door, or if they are not rigid structures and have differently shaped articular surfaces. In birds, the basitemporal articulation lies behind the complex quadrate hinge, not in line with it, but has a flat articular surface and/or thick, flexible articular pads. The two jaw articulations of *Diarthrognathus* lie next to one another and along the same axis of rotation; consequently, the lower jaw can swing without any difficulity. However, two separate suspensions of the mandible may hinder certain actions of the jaw, thereby being less advantageous than a single pair of hinges. In birds, the basitemporal articulation is decidedly smaller than the quadrate hinge and unable to acquire the function of jaw suspension. In the mammal-like reptiles, the coronoid process was much larger than the articular-quadrate hinge and probably better able, from the moment it touched the squamosal, to assume the role of jaw suspension. The new articulation would be better aligned with the pull of the powerful temporal muscles and consequently would provide a steadier support for the mandible. A shift in the relationship between the mandible and the rest of the skull probably occurred at the time the coronoid process abutted against the squamosal and assumed the role of jaw suspension. This shift of the mandible may have broken the contact between the articular and the rest of the mandible, thereby leaving the quadrate, articular and angular lying free in the proximity of the middle ear. Once started, the change from the old suspension to the new one could have been quite rapid and abrupt, which might explain, in part, the rarity of fossils showing both the old reptilian and the new mammalian jaw articulations. Although the above explanation postulates rapid shifts in certain phases of the evolution of the mammalian jaw suspension, it is still in agreement with Watson's conclusion (1953, pp. 176–177) that the entire process took place gradually and that there is no reason to invoke macromutations to explain any step in the evolution of the mammalian jaw articulation.

This new jaw suspension was only a byproduct (i.e., dependent upon the changes invoked by independent selection forces) of a whole series of modifications brought about by the change in the method of feeding, but proved to be so successful that it became one of the most important features in the evolution of the mammals. The evolution of the mammalian arrangement of the ear ossicles—the addition of two bones to the one already present—occurred after the articular and quadrate were no longer concerned with support of the mandible and again as a by product of an independent evolutionary change, namely the evolution of the mammalian jaw hinge (see Watson, 1953). Hence, two of the diagnostic features of the mammals developed as byproducts of other adaptations, and only after they had evolved did they acquire their great importance in the evolution of the mammals.

There is, still, a conflict of opinion on whether the mammalian jaw articulation is monophyletic or polyphyletic. Patterson (1956, p. 98 and figure 17) supports the earlier views of Simpson and of Olson and implies that several lines of therapsid reptiles acquired the mammalian jaw hinge independently. In his figure 17, he shows three crossings of the reptilian-mammalian border (acquisition of the mammalian jaw hinge) and implies a fourth. On the other hand, Kühne (1956, p. 142) concluded that: "The morphological changes involved in the evolution of the mammalian middle ear and jaw articulation were essential [to the evolu-

tion of the mammals]; to bring it about, many correlated skeletal changes had to occur; it was probable therefore that the transition took place only once. In my opinion the Monotremes did not evolve independently from the rest of the mammals." Which view is correct cannot be determined at present, but the evolution of the avian basitemporal articulation suggests that the mammalian jaw articulation and consequently the ear ossicles could have evolved several independent times. If a similar change in feeding habits had occurred independently in several parallel lines of therapsids, then could not a similar change in the structure of the mandible take place? This has happened in the birds, where the enlargement of the medial process of the mandible and the subsequent evolution of a basitemporal articulation has taken place in a number of unrelated lines. Indeed the existing variation of the basitemporal articulation in the entire class of birds can be regarded as illustrating the situation of the therapsid reptiles at the time of the "reptile-mammal border," i.e., the rise of several lines in which the same morphological change—development of a new jaw articulation while the old one was still functional—took place.

To conclude, evidence gathered from a consideration of the evolution of the avian basitemporal articulation supports the view that the mammalian jaw articulation evolved by gradual steps and quite possibly came into being several independent times.

Preadaptation

The evidence briefly presented above has, it seems to me, a decided bearing on the important, but highly controversial subject of preadaptation. Ever since Dohrn formulated his "principle of functional change" in 1875 (see Russell, 1917, pp. 274–278), workers have disagreed on the significance of preadaptation. Some workers have denied its existence, but this view can be discounted at once, for there are many unquestionable examples of preadapted structures. Much of the controversy has resulted from changes in the meaning of the term. The term "preadaptation" was coined (Simpson, 1953, pp. 134–135) to describe those mutations which were not immediately beneficial, but which would be useful to the animal in the future. Over the years, the meaning of preadaptation has broadened to include structures instead of mutations only, until today it is equivalent to Dohrn's "functional change." Assuming that preadaptation is a real evolutionary phenomenon and that the term is used in the "modern sense," the remaining controversies can be grouped under two main headings: (a) what is the significance of preadaptation in evolution?, and (b) what is the "mechanism" of preadaptation?

The answer to the first question is still largely a matter of opinion. Most workers would agree without question that preadaptation has played a part in the origin of many structures; however, only a few workers (e.g., Simpson, 1953, p. 189) claim that "preadaptation is practically universal." My feeling is that the latter view is correct; in fact it would be reasonable to postulate that the evolution of most, if not all, new structures involved old structures which were preadapted for the new function. The correctness of this opinion can be resolved only by extensive surveys of the evolution of new structures to determine what percentage involve preadaptation. Assuming that preadaptation was involved in the origin of most structures, I would go further and claim that a thorough understanding of preadaptation is prerequisite to the solution of many other problems of macroevolution. Indeed, it is likely that many seemingly difficult problems would vanish were preadaptation completely understood. An example of such problems is the old one of how can selection act on a structure before that structure has appeared?, or, conversely, how can a structure be selected for before it has acquired a selective value

(see Romer, 1949, pp. 105–107)? It will be shown later that if a new structure developed from an old one serving in some other capacity but preadapted for the new function, then the structure is already present and available to the new selection force. Another example is the question of which came first, the form or the function of a structure? I do not intend to discuss these questions in detail; they are beyond the scope of this paper and were offered only to illustrate the importance of understanding preadaptation before studying many other problems of evolution.

The answer to the second problem, the "mechanism" of preadaptation, has been and still is largely a matter of opinion, but it need not be. Probably the basis for much of the disagreement on the significance of preadaptation has been the failure of most workers to understand its operation and that in turn stems from the lack of clear definitions of preadaptation. Two of the best discussions of preadaptation published in recent years are those of Davis (1949, pp. 82–87) and Simpson (1953, pp. 188–198), yet neither author defines preadaptation. Rather they separate their examples of preadaptation into a number of categories, which only leads to greater confusion. Some of these categories state the same thing in slightly different ways, as for example, Simpson's categories 4, 6 and 8 or categories 5 and 7. More important is that some of these categories (Davis' category 1, and Simpson's categories 5 and 7) are not really preadaptation, but are close to or even identical with postadaptation. Associated with this lack of precise definitions of preadaptation is a confusion of the selection forces associated with preadaptation and postadaptation of the same structure, and whether preadapted structures are adaptive in themselves. Usually only the vague term "selection" is used with no idea as to what is being selected for and why. Clearly it is necessary to first define preadaptation and then outline in detail its "mechanism."

The definition of preadaptation that I shall adopt is close to Dohrn's original one and to the one implied by most authors. *A structure is said to be preadapted for a new function if its present form which enables it to discharge its original function also enables it to assume the new function whenever need for this function arises.*

The selection forces responsible for molding a structure into a preadapted form are *always* those associated with the original function of the structure. Needless to say, the acquisition of any particular preadapted form by a structure is strictly fortuitous. The original selection force may continue to operate after the preadapted structure assumes its new function and is under the control of the new selection force because of the simple fact that a structure may simultaneously have a number of different functions. For example, the medial process of the mandible continues to serve its original function (a point of insertion for certain jaw muscles) after it becomes part of the medial brace and is thus still under the control of the selection forces associated with the strength of the jaw muscles. Any change from the preadapted form to one enabling the new structure to better execute its new function (postadaptation) is under the influence of the selection forces associated with this new function. These selection forces cannot act until the structure becomes preadapted. However, one should not assume that the structure becomes preadapted first and that the need for the new structure (the selection force) arises afterwards. The selection force for a new structure may be in existence long before the structure is available to them, that is, before the structure is preadapted. Apparently in both the birds and the late mammal-like reptiles, the need for a brace of the mandible developed before an ascending process of the mandible became long enough to touch the base of the skull. This sequence of the need arising before the structure becomes pre-

adapted may account for the sudden and rapid evolution of a new character or kind of animal—"explosive evolution." The new selection force would seize the structure the moment it becomes preadapted; the new structure evolves and the animal is at last able to assume the new function and possibly exploit a new niche.

A clear separation of the selection forces associated with pre- and postadaptation may help to rectify the difficulties in Davis' category 1 and Simpson's categories 5 and 7. I have stated above that these examples are postadaptation, not preadaptation. These authors describe changes in already existing structures without any apparent change in function, especially the example of the *Aptenodytes* penguins. In any phyletic line, postadaptive changes in one species would be the preadaptive changes in the evolution of its descendent species and so on. If these dubious examples were redescribed, taking care to distinguish between the selection forces and to note which are postadaptive and which are preadaptive changes, then the difficulties as to whether these examples illustrate pre- or postadaptation would fade away.

One of the most controversial problems of preadaptation is whether preadapted structures are adaptively oriented (see Simpson, 1953, footnote on p. 196). There are many preadapted structures that are unquestionably adaptive, but some workers hold to the belief that preadapted structures may be neutral or inadaptive in the ancestral species. If, as outlined above, preadapted structures are molded by the selection forces associated with the *original* function of the structure, then they must be adaptive. This is in agreement with Simpson's conclusion (1953, top of p. 194) that preadapted structures are adaptively oriented. If, however, some other agency (e.g., genetic drift) was involved in the formation of a preadapted structure, then it is possible for a preadapted structure to be neutral or even inadaptive. I would doubt that any agency other than selection has a significant part in the formation of a preadapted structure. Simpson (1953, pp. 194–198) claims, however, that genetic draft may have an important part in the evolution of some preadaptive structures, hence there would be an inadaptive phase in the origin of new structures. His discussion leaves me somewhat confused as to the importance of the "inadaptive phase" in the evolution of new structures, although he clearly states that preadaptive structures are adaptive.

Turning again to the basitemporal articulation of birds, we have seen that the medial process of the mandible, originally enlarging to provide a greater area for the attachment of certain jaw muscles, was preadapted to provide a brace for the mandible because of its close proximity to the base of the skull. Similarly, the lateral and medial processes of the basitemporal plate had developed originally to provide bony knobs for the attachment of certain cervical muscles, but were preadapted to provide a suitable anchorage for the medial brace because of their position and their projection below the rest of the basitemporal plate. All of these processes retained their original function after the new function of mandibular support was superimposed on them. Likewise, in the evolution of the mammalian jaw articulation, the coronoid process developed in response to the selection force for a stronger temporal muscle. but at the same time, it became preadapted to provide a supporting brace for the mandible. The articular and quadrate bones of the early mammals lay in the otic region and once they were freed of their original role of jaw suspension, they were preadapted to take part in the vibration-transmitting structure of the mammalian middle ear. Therefore, every feature involved in the avian medial brace, the mammalian jaw articulation and the mammalian ear ossicles, had a previous function and became preadapted for its new function while being modified to better execute its original function;

the entire process was adaptive considering both the structures and the animals involved.

Genetics of preadaptation: The application of preadaptation to the origin of new structures has some interesting genetical repercussions. Simpson (1953, p. 195) has already commented on the fact that certain adaptive changes resulting from preadaptation can occur without any genetical change. This can be generalized to cover all adaptive changes resulting from preadaptation. By definition, preadapted structures are capable of preforming their new function, thus they can assume this new function whenever the need arises without any morphological and genetical modifications. It is not necessary to postulate the emergence of a new structure from new mutations or recombinations of existing genes to meet the demands of the new selection force. If a structure is preadapted for this new function, then the structure is already present and functioning; hence it is available to the selection forces associated with the new function. These new selection forces simply seize the preadapted structure and modify it so that it can better execute its new function. But this is postadaptation; the structure is already present and functioning. The actual "origin" of the new structure, which can be defined as the acquisition of the new function by the preadapted structure, was not accompanied by a genetical change.

Genetics of the basitemporal articulation: The evolution of the basitemporal articulation illustrates a special and perhaps rare case of the general genetical situation just described. In the above discussion, the preadapted structure has a direct genetical basis at the time it becomes preadapted, in the case to be described, the preadapted structure does not have a genetic basis and only acquires one after assuming its new function. This special case may, however, be a problem of the proper delineation of characters and the genetical control of development rather than a problem of preadaptation.

When we speak of an articulation, we mean the system of morphological features which enable two bones to meet and move on one another. Although modifications in existing articulations may result from mechanical influences, the ontogenetic development of normal articulations in vertebrates is under direct genetical control (see above). Therefore, the basitemporal articulation may be considered as a morphological structure whose ontogeny is under direct genetical control. Hence we should be able to speak of its evolution in the usual terms of genetical variation and selection in favor of those variants leading toward the basitemporal articulation. Can we do so? I think not.

In the above discussion of the evolution of the basitemporal articulation, I have been very careful not to speak of the actual evolution of the articulation, but always of the medial brace composed of the medial process of the mandible abutting against the base of the skull. I have at no time stated or implied that there were genetically controlled variants leading toward the basitemporal articulation which were favored by selection, but rather spoke of the genetically controlled modifications in the medial process of the mandible and how selection acted on these modifications. It seems entirely reasonable to suggest that there was no direct genetical basis for the basitemporal articulation when it first appeared, or even when it reached the advanced structural stage found in the skimmer. Rather, the basitemporal articulation was at first the obligatory phenotypic result of the medial process of the mandible abutting against the base of the skull—the inherent physiological consequence of two bones moving on one another. Yet a direct genetical control for the basitemporal articulation no doubt developed at some time after the articulation first appeared. This genetical control could have been brought about by the process of stabilizing selection as defined by Schmalhausen (1949, pp. 78–79). On the same basis,

I would suggest that, in the evolution of the mammalian jaw articulation, there was also no direct genetical basis of the *articulation itself* until some time after it had appeared, and perhaps even after it had served as the sole functional jaw hinge. Again genetical control of the ontogenetical development of the mammalian jaw articulation was most likely brought about by stabilizing selection.

Stabilizing selection is simply the process by which the control of development by the genotype is increased at the expense of the role of the environment. In the cases of the avian basitemporal articulation and the mammalian jaw articulation, the environmental factor is the length of the ascending mandibular process. If the mandibular process in birds abuts against the base of the skull, the basitemporal articulation can develop, and the medial brace will form. In the early mammals, the development of the jaw suspension was dependent upon the coronoid process abutting against the squamosal. If the mandibular process fell short of the base of the skull, the medial brace or the jaw suspension could not develop in the absence of direct genetical control for the articulation. Those individuals in which this occurred would then be eliminated by selection. Those individuals that had acquired a genetical control of the articulation—a chance phenomenon—would be assured possession of these structures even in the event of the mandibular process falling short of the base of the skull and thus would be favored by selection. These latter individuals will gradually spread through the population until in time the entire population has gained genetical control of the ontogeny of the articulation.

Multiple Pathways of Evolution

The variation in the structure of the medial brace between groups of birds (outlined below) suggests another problem of evolution—namely the adaptive answers to the same selection force. We usually divide the origin of a structure into two steps: first the appearance of a new selection force, and second the development of some structure to meet the demands of this selection force. However, is there but one structure that can meet the demands of a particular selection force or may there be several or even many possible adaptive responses to one selection force? Many workers have assumed that the former alternative is true, but Rensch (1954, pp. 64–74) and Simpson (1953, pp. 168–181, especially, pp. 179–181) have shown that the latter view is correct. They have termed this phenomenon "directionlessness" or "opportunism" in evolution and have cited a number of examples that demonstrate the variability of the adaptive answers to the same selection force. One of the most important consequences of "directionlessness" is that the differences between taxonomic groups may be nonadaptive. This is of prime concern to functional anatomists, some of whom make the basic assumption that all of the morphological differences between the animals under observation have a functional meaning. I shall return to this point later.

The use of the term "directionlessness" and to a lesser extent "opportunism" in evolution carries with it the implication that the adaptive paths chosen by the organisms are essentially random. This is not true, for the path taken by a specific organism depends to a large extent upon its past history. I would prefer to term this principle *"multiple pathways of evolution* or *adaptation"* which carries with it no implication of randomness. The working of this principle would be as follows. *The same selection force acting on a group of organisms may elicit different adaptive responses depending upon the differences in the genotypic and phenotypic characteristics of the organisms.* These different adaptive responses would be the multiple pathways of evolution or adaptation. Whichever path is taken by a specific organism is determined by the

characteristics of that organisms; hence the operational level of the principle of multiple pathways is on the specific level. However, its operation can be more easily demonstrated when we observe the results of the same selection force acting on a group of related, but varying organisms.

Returning again to the evolution of the medial brace in birds, I have shown above that the selection force guiding its evolution is stress on the quadrate hinge when the bill is opened. How have birds responded to this selection force? Have they all developed a medial brace and basitemporal articulation similar to that described for the skimmer? The answer is no. The medial brace may develop, but its structure varies. (I do not consider here the adaptive pathways that do not involve the medial brace, such as development of a stronger quadrate hinge or strengthening of the jaw muscles.) The medial process of the mandible is always part of the brace, but it may articulate with different processes of the basitemporal plate. The medial process of the mandible may articulate with (Bock, Unpublished):

a) The anterior edge of the lateral process of the basitemporal plate, as seen in the Apterygidae, the Gruidae and their allies, and some rails. With the possible exception of the Apterygidae (which may, however, be derived from the rails), these families are all related, so that the similarity in the basitemporal articulation is probably due to common ancestry.

b) The ventral edge of the lateral process of the basitemporal plate. This is the commonest type and is found in the turkey vulture, Sagittariidae, *Cochlearius*, Musophagidae, the gallinules, the plovers, gulls, skimmers and their allies, Pteroclidae, Raphidae, Caprimulgidae and Coliidae. Most of these forms are unrelated, so that the similarity in the medial brace is due to similarity in structure, not common ancestry.

c) The medial process of the basitemporal plate, as seen in the Spheniscidae, some Tubinares, Phalacrocoracidae, Sulidae, Falconidae, some Old World vultures and the larger New World vultures. Again most of these forms are unrelated and thus the similarity in the medial brace is due to the similarity in the morphology of the skull.

Hence it is the structure of the basitemporal plate that determines the particular pathway a species will take when it acquires a medial brace. As the medial process of the mandible grows towards the base of the skull, it will tend to abut against that basitemporal process projecting the farthest below the base of the skull. Hence, whether the lateral or the medial process of the basitemporal plate becomes part of the medial brace in a particular species depends upon which one was better developed (for independent reasons such as attachment of certain cervical muscles) at the time the medial process of the mandible became long enough to establish contact with the base of the skull. The fact that a similar medial brace may be present in a group of related families is consistent with the principle of multiple pathways. These families would, in general, be more similar to one another in the morphology of their skull than a group of unrelated families and, if the same selection force was acting on all, the resulting adaptation, even though independently acquired, would be rather similar. On the other hand, the more divergent members of a group may have a different type of brace from that found in the rest of the family, e.g., the gallinules and coots in the Rallidae, the large condors as compared to the smaller species of New World vultures, and *Cochlearius* in contrast to the rest of the herons. These species differ sufficiently in their skull structure from the other members of their family so that they would respond differently to the same selection force.

The concept of multiple pathways is of the greatest importance in studies of adaptation and systematics. For ex-

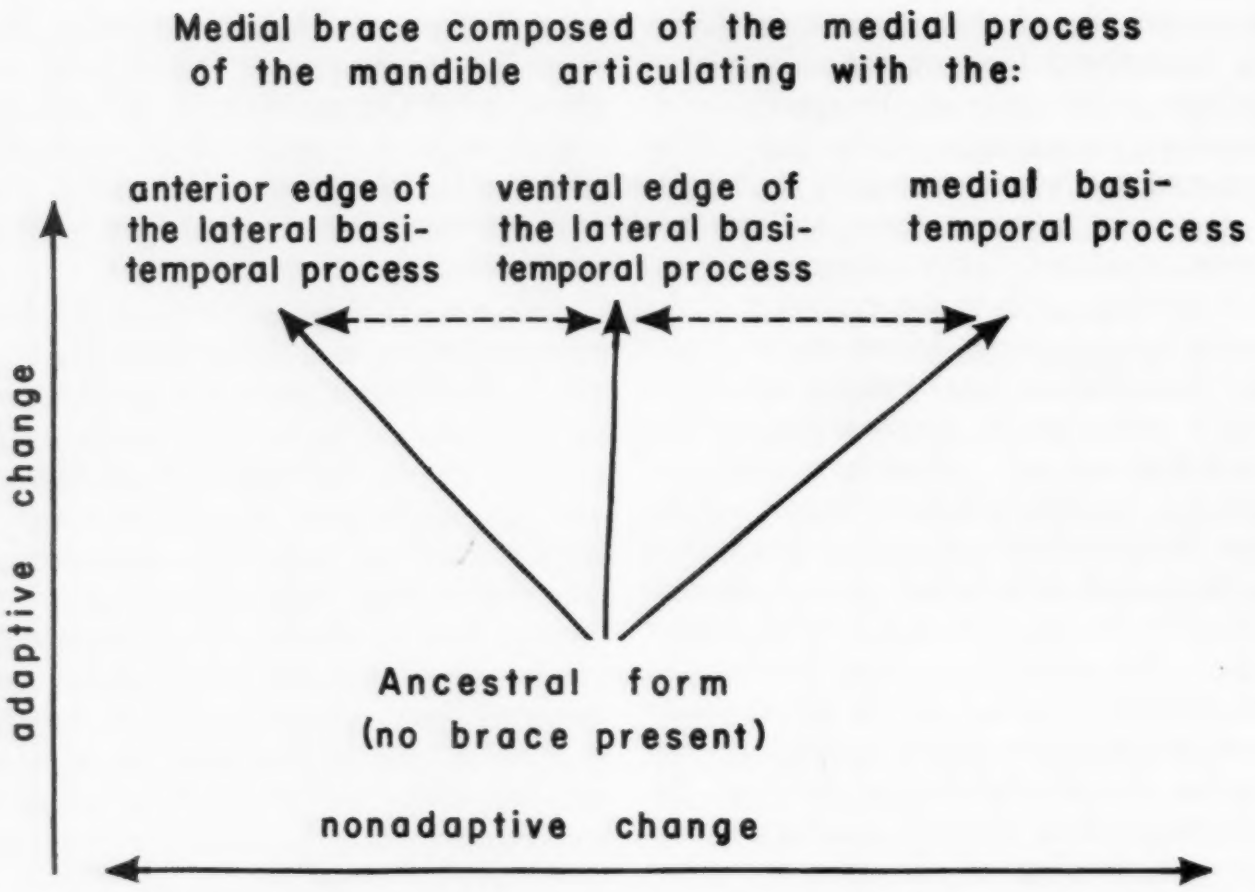
Medial brace composed of the medial process of the mandible articulating with the:
anterior edge of the lateral basi-temporal process
ventral edge of the lateral basi-temporal process
medial basi-temporal process
adaptive change
Ancestral form
(no brace present)
nonadaptive change

FIG. 4. Multiple pathways of evolution or adaptation in the evolution of the medial brace. See text for explanation.

ample, a functional anatomist may study several genera of the same family and assume that all of the observed morphological differences between these genera have a functional significance and hence they are adaptive differences. This assumption is incorrect and has led students of functional anatomy into erroneous conclusions such as, for example, the conclusion that several structures are nonadaptive simply because their morphological differences are nonadaptive. Simpson (1953, pp. 161–181) has discussed the problem of nonadaptive differences between contemporaneous taxonomic groups in great detail. He points out that there are many differences between taxonomic groups "which seem most probably to be nonadaptive *as differences.*" (p. 179, italics mine), and goes on to emphasize (p. 180) that only when two species are actually competing with one another will the *differences* between these species that arise as a result of their competition be adaptively oriented. In all other cases, only the differences between the ancestral and the descendant groups are adaptive; the differences between the several descendent groups are nonadaptive. As an example, the major variations in the structure of the medial brace are not the result of functional differences in the medial brace; the brace protects the quadrate hinge no matter which process of the basitemporal plate articulates with the medial process of the mandible. The morphological differences between the several types of medial plate simply depend upon which process of the basitemporal plate was best developed at the time the medial process of the mandible established contact with the base of the skull—a historical chance and nonadaptive in terms of the medial brace. (This is not to say that the differences in the basitemporal plate are not adaptive; they are, but because of totally independent reasons, i.e., the insertion of cervical muscles.) Yet, each type of medial brace is definitely adaptive be-

cause it functions as a brace and, as Simpson has emphasized, it is erroneous to conclude that several structures do not have adaptive significance just because their morphological differences are not adaptive. This conclusion can be translated into terms of multiple pathways by stating that (see fig. 4) the changes along any one of the multiple pathways of evolution (solid lines) are correlated with functional needs and hence are adaptive changes, but that the gaps between the pathways or shifts from one pathway to another (if they exist, dashed lines) are nonfunctional and hence nonadaptive in terms of the medial brace.

Near the completion of this study, a possible source of confusion because of similarity in terminology was discovered between the concept of multiple pathways of evolution and the idea that several adaptations can evolve in the same animal in response to one selective demand. Mayr (1956, p. 107) in discussing the problem on one solution versus several solutions for the same selective demand on an animal, concluded that: "Multiple solutions for biological needs are the general rule in evolution." However, Mayr's "multiple solutions" are not the same as "multiple pathways of adaptations"; these are different evolutionary problems. He is considering several adaptations for the same need in one species, while I am considering the several ways in which different species can adapt to meet the same selective demand, but only one of these adaptations would be found in a single species. The simplest solution to this problem would be to change Mayr's "multiple solutions" to "multifactoral solutions" or a similar term which would clearly indicate that these are additive adaptations for the same need in one species. This is not just a semantic problem because a member of a set of multifactoral solutions may also be a member of a set of multiple pathways of evolution. For example, insurance against the disarticulation of the mandible in birds may be supplied by the combination of the quadrate hinge, the jaw muscles, various ligaments and the medial brace of the mandible—these would constitute a multifactoral solution. But, as has been shown above, the medial brace of the mandible can take several forms: hence it would make up a set of multiple pathways of evolution.

An Evolutionary Model

A two dimensional graph (fig. 5) may serve as a model to illustrate the steps in the origin of a new structure and to summarize the ideas advanced in this paper. The following discussion will be highly formal, almost to the point of pedantry, but I believe that a precise presentation of the factors involved in macroevolutionary changes may aid future work in this field. Again, I must emphasize that I am dealing only with preadaptation and multiple pathways of evolution; I am not concerned with macroevolutionary changes that do not involve preadaptation.

In this model, morphological change (phenotypic only, genotypical change is not considered in this model) is shown along the horizontal axis, evolutionary change along the vertical axis. Evolutionary change is defined, for the purposes of this model, as modification in the operational ability of a structure or an organism (i.e., change in adaptation). Since this is a theoretical model, I shall employ only straight lines. The selection forces associated with the evolution of a new structure are shown along the vertical axis; the two sets are assumed to be independent of one another. Selection force 1 controls the evolution of the original structure up to the preadapted level. It may have partial control over the new structure if the structure retains its original function after acquiring the new function. Selection force 2 is associated with the new function and controls the evolution of the new structure. It may be present, but cannot act before the old

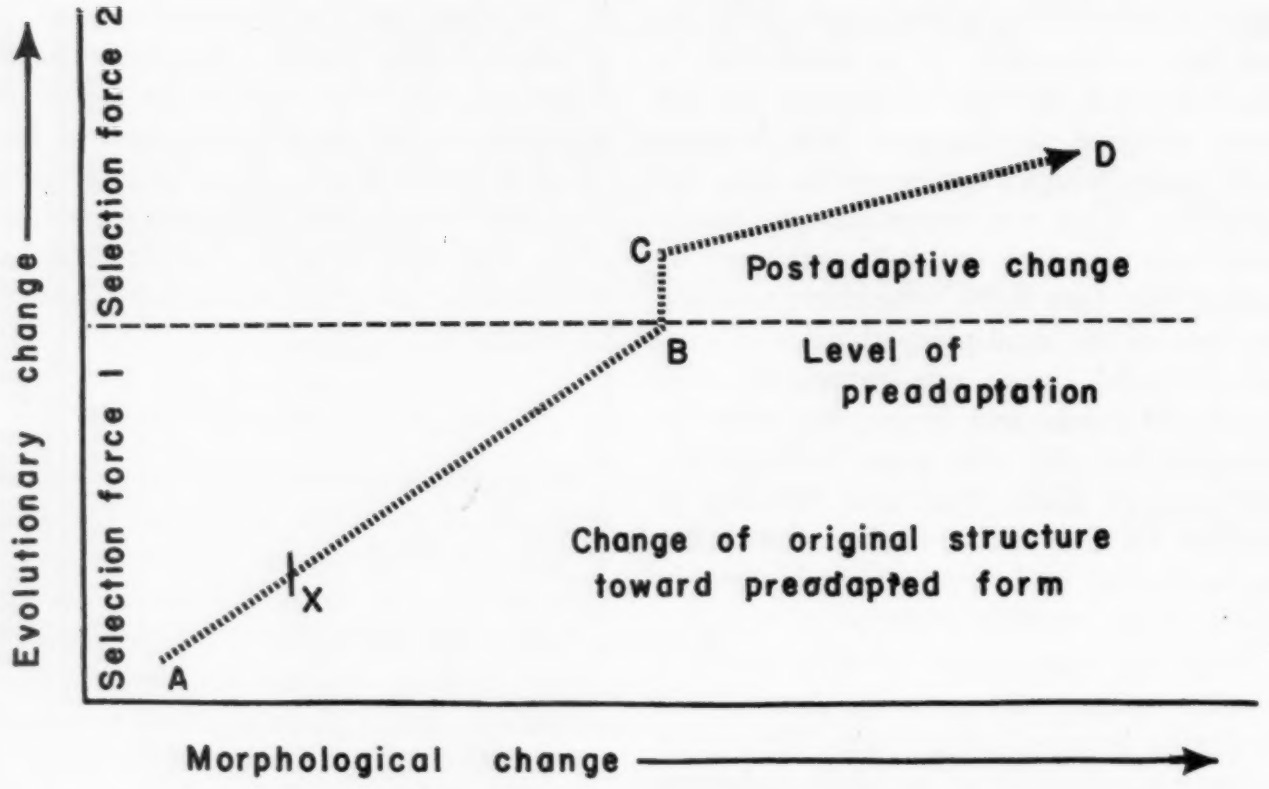

FIG. 5. Model of macroevolutionary change. See text for explanation.

structure has become preadapted. Time is not considered in this model.

Let us start with a structure at point A and trace the steps leading to the origin and subsequent evolution of a new structure. Under the control of selection force 1, the structure moves toward point B in a typical pattern of gradual evolution. Upon reaching point B, the structure becomes preadapted for the new function and can be seized by selection force 2 whenever that selection force appears. If the new selection force already exists, then it would seize the old structure the instant it reaches the preadapted level. The next step might be considered the actual "origin" of the new structure, namely the acquisition of the new function by the preadapted structure, which results in an immediate evolutionary change with little or no morphological change, as shown by the vertical line B – C. The new structure is now under the control of selection force 2 and becomes further specialized (postadapted) for this new function by gradual steps toward point D.

The "abrupt shift" present in the evolution of many new structures is usually believed to be a morphological change, but it is really a shift in function. The nature of this functional shift can be easily understood if we regard the level of preadaptation as a threshold which the old structure must reach before the new structure can evolve. This use of "threshold" is not the same as Simpson's usage (1953, pp. 196–197). The old structure has reached the threshold by gradual evolutionary steps under the control of selection force 1; however, it must be remembered that the evolution of a structure toward the preadapted level associated with another function is strictly fortuitous. At the threshold level, the preadapted structure has already acquired the necessary morphological form to assume the new function. In fact, one could also say that the preadapted structure is already functional, but that this function does not become obvious until it has acquired a selective value, i.e., the need for this function has arisen. Thus the preadapted level is a threshold at which there is a functional shift, not a morphological shift. Because this shift has great

functional and evolutionary significance, it may appear that it also involves a large morphological change; however, this "morphological change" is more apparent than real.

If the above suggestion that the origin of most or all new structures involves preadapted structures is correct, we may have to change or rather refine some of our standard evolutionary phraseology. We usually say that in the evolution of a new structure, selection favors any genetical variants leading toward this new structure; however, by selection we imply the selection forces associated with the new function. This implication is not correct *if* the new structure develops from a preadapted structure. I have just postulated that a preadapted structure, by definition, is capable of performing its new function before the need for this function arises (i.e., before the new selection force acts). The evolution of the old structure toward the preadapted condition is under the control of the selection forces associated with the original function of this structure. This structural change increases the ability of the old structure to execute its original function and has nothing to do with the new function. Thus the new structure "appeared" in a morphological sense as a result of the action of the old selection forces, not of the new selection forces. Therefore, while it is still true to say that evolutionary change is by selection acting on genetical variants, the exact mechanism involved in the origin of a new structure is more subtle than that implied in the beginning of the paragraph. What should be said is that the old selection forces modify the original structure until it reaches the preadapted level. At this point, the preadapted structure can assume its new function; hence it has "appeared." Then the new selection forces modify the new structure so that it can better execute its function (postadaptation), but they have nothing to do with the origin of the new structure. This line of reasoning forces us to say that the origin of a new structure is not as might be expected under the control of the selection forces associated with the new function, but is actually under the control of the selection forces associated with the original function of the old structure. This stated sequence of events is simply the natural extension of the well known fact that evolutionary changes carry along with them structural changes (= evolutionary potentials) other than those which are being selected.

Multiple pathways of evolution can be illustrated on this evolutionary model (but are not shown here in order to preserve the simplicity of the model) by tracing the evolution of the same structure in a number of species instead of just one. If selection force 1 acts on all of these species, the structure would change and move toward the preadapted level in some species, but not necessarily toward only one point B. Rather, the preadapted structures of the several species could differ one from the other and could be represented by a series of points, B_1, B_2, B_3, and so on. The final result could be a series of postadapted structures, D_1, D_2, D_3, etc., differing from each other morphologically, but having the same function. These evolutionary paths would be the multiple pathways of evolution.

When the evolution of a new structure is traced from the old structure at point A to the new structure, the steps are easy to determine and analyze. There is, in theoretical discussions, little danger of missing a step for they follow one another in a smooth and steady sequence and the omission of any step is at once noticeable. I shall not repeat the steps in the evolution of the avian basitemporal articulation or the mammalian jaw articulation using this model; a little reflection on the evolution of these structures will suffice to show that this model fits their evolution.

This evolutionary model also reveals the difficulties encounted when attempting

to explain macroevolutionary changes by following evolutionary lines backwards. These difficulties usually arise because workers either forget to consider the changes between points A and C or err in their analysis of this segment of the evolution of a new structure. Commonly, selection force 1 is forgotten and the entire evolution between A and D is thought to be under the control of selection force 2. Upon further study, however, it is usually discovered that the early part of the evolution of the new structure cannot be explained in terms of selection force 2 (consider the basitemporal articulation) and consequently an inexplicable gap is left. More often, the structural change between some point on the line between A and B, say X and point C is ignored; hence there is a morphological gap between the old and new structures which cannot be explained by current evolutionary theories. It is these supposed inexplicable gaps for which many unacceptable theories of macroevolution have been advanced. These theories usually invoke large genetical modifications or the acquisition by means of genetical drift in small populations of a structure that may be disadvantageous for the organism, but preadapted for the new function. However, in both instances, the solution to the problem lies in understanding fully the changes that take place in the evolution of a new structure, not in looking for theories to explain these supposed large structural gaps. The problems associated with macroevolutionary changes are not as much genetical or populational ones as they are the determination of the functional significance of structures and the establishment of correct historical sequences. If the steps in the evolution of a new structure are properly established and analyzed as outlined in the above evolutionary model, then the current concepts of gradual evolutionary changes will prove to be sufficient to explain the origin of almost every, if not every new structure.

Summary

1) The basitemporal articulation of birds forms the hinge between the bones of the medial brace of the mandible. This brace consists of the medial process of the mandible abutting against the basitemporal plate and serves to prevent the disarticulation of the quadrate hinge because of strong forces on the mandible when the bill is opened.

2) The evolution of the medial brace is outlined. It is shown that the medial process of the mandible increases in length in connection with increasing strength of the jaw muscles. In some groups, the medial process finally abuts against the base of the brain case with the basitemporal articulation developing where the two bones came into contact. Increase in the length of the medial process of the mandible and the subsequent development of the medial brace occurred in many independent lines of birds.

3) The evolution of the medial brace is compared to the evolution of the mammalian jaw articulation. Again, a process developed on the mandible of the mammal-like reptiles in response to a selection force for stronger jaw muscles. The process finally touched the brain case and first formed a brace for the mandible and then assumed the role of jaw suspension. Analogy from the evolution of medial brace argues in favor of the hypothesis that the mammalian jaw hinge evolved several independent times.

4) The concepts of preadaptation and multiple pathways of evolution are discussed. It is suggested that the evolution of most new structures involves old structures which are preadapted for the new function. The preadapted level is a threshold at which there is a functional shift, not a morphological shift. If the selection force for a new function acts on a group of organisms, the resulting adaptations do not have to be similar, but may vary in structure. Because the morphological differences between these sev-

eral adaptive answers are nonadaptive, these differences must not be explained on functional grounds.

5) A model of macroevolutionary change is presented. The major conclusion drawn from this model is that if the functional significance of structures are properly analyzed and correct historical sequences were established, then the evolution of most, if not all, new structures can be explained on the present concept of gradual evolutionary change.

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Literature Cited

Bock, W. J. Unpubl. The basitemporal articulation in birds. Ms.

Crompton, A. W. 1958. The cranial morphology of a new genus and species of Ictidosauran. Proc. Zool. Soc. Lond., **130**: 183–216.

Davis, D. D. 1949. Comparative anatomy and the evolution of vertebrates. *In* Jepsen, G. L., *et al.*, Genetics, Paleontology and Evolution, pp. 64–89.

Kühne, W. G. 1956. The Liassic therapsid *Oligokyphus*. London, British Museum (Natural History), x + 149 pp.

Kuhn-Schnyder, E. 1954. Der Ursprung der Säugertiere. Vierteljahrsschrift. Naturfor. Gesell. Zürich, **99**: 165–197.

Mayr, E. 1956. Geographical character gradients and climatic adaptations. Evolution, **10**: 105–108.

Murray, P. D. F. 1937. Bones. Cambridge, England, x + 203 pp.

Patterson, B. 1956. Early Cretaceous mammals and the evolution of the mammalian molar teeth. Fieldiana; Geology, **13** (1): 1–105.

Rensch, B. 1954. Neure Probleme der Abstammuntslehre. Die transpezifische Evolution. 2nd Edition, Stuttgart, xi + 436 pp.

Romer, A. S. 1949. Time series and trends in animal evolution. *In* Jepsen, G. L., *et al.*, Genetics, Paleontology and Evolution, pp. 103–120.

Russell, E. S. 1916. Form and function. A contribution to the history of animal morphology. London, vi + 383 pp.

Schmalhausen, I. I. 1949. Factors of evolution. The theory of stabilizing selection. Philadelphia, xiv + 327 pp.

Simpson, G. G. 1953. The major features of evolution. New York, xx + 434 pp.

Watson, D. M. S. 1953. Evolution of the mammalian ear. Evolution, **7**: 159–177. 159–177.

SPECIATION IN BUTTERFLIES OF THE *PAPILIO GLAUCUS* GROUP. II. ECOLOGICAL RELATIONSHIPS AND INTERSPECIFIC SEXUAL BEHAVIOR[1]

LINCOLN P. BROWER

Department of Zoology, Yale University[2]

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Papilio glaucus Linné and four allied Tiger Swallowtail butterflies, *P. alexiares* Hopffer, *P. eurymedon* Boisduval, *P. multicaudatus* Kirby, and *P. rutulus* Boisduval, form a group of closely related species which are limited to North America. Three of these, *P. eurymedon, P. multicaudatus,* and *P. rutulus,* are extensively sympatric in western North America and have been shown to be morphologically closer to each other than any one is to the eastern and northern *P. glaucus.* For these reasons, it was concluded that they have probably had a common descent from subdivisions of a southwestern Pleistocene isolate, whereas *P. glaucus* has descended from an isolate in the southeast (Brower, 1959). The purpose of this paper is to present the results of three summers' field studies which were carried out in the western United States in order to investigate the adult interrelationships of the three sympatric species in their natural environment. The study is divided into two parts; the first describes the ecological relationships and the second, interspecific sexual behavior.

1. ADULT ECOLOGICAL RELATIONSHIPS

The method used to compare the autecologies of the butterflies was to establish stations along the creeks at different altitudes in two western canyons where frequency data on each of the species were collected over a period of days. The first area chosen for study was Left Hand Canyon which is in the Front Range of the Rocky Mountains in Boulder County, Colorado. The headwaters of Left Hand Creek are on Niwot Mountain at an altitude of approximately 9,500 feet and the canyon descends eastward for a distance of 18 miles to the plains which are at an altitude of 5,700 feet. Although the canyon has few human inhabitants, parts of the natural vegetation were burned off by forest fire and/or were lumbered around 1900 so that large areas are not climax associations. Larval foodplants suitable for *P. multicaudatus* (*Prunus virginiana* Linné) and *P. rutulus* (*Salix* spp., *Populus* spp.) were present in abundance at or near each of the areas where observations were made, and that of *P. eurymedon* (*Ceanothus fendleri* Gray) was also found near each, but was most flourishing between 6,500 feet and 8,500 feet on the south-facing slopes. Three stations were selected in Left Hand Canyon at the following altitudes: Station 1, in the foothills zone at 5,900 feet; Station 2, in the lower montane zone at 6,950 feet; and Station 3 at 9,300 feet in the upper montane zone.

Specimens were netted in the air or while feeding at flowers and each was given a consecutive number designated by applying from one to three dots of combinations of five different colors of cellulose paint towards the base of the underside of the wings. With the exception of a few which were injured or removed from the population in order to obtain eggs, all the butterflies caught in Left Hand Canyon during both years

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[2] Present address: Department of Biology, Amherst College, Amherst, Mass.

TABLE A. *Hourly trend of flight up and down canyon in Big Cottonwood Canyon, Utah, at Station 1*

Time (R.M.S.T.)	18 July 1955				19 July 1955			
	P. multicaudatus		*P. rutulus*		*P. multicaudatus*		*P. rutulus*	
	Up canyon	Down canyon	Up canyon	Down canyon	Up canyon	Down canyon	Up canyon	Down canyon
A.M.								
8:00– 9:00	3	5	9	5	5	6	3	5
9:00–10:00	9	6	5	9	3	9	6	7
10:00–11:00	7	10	2	6	5	9	1	10
11:00–12:00	1	5	3	3	3	1	0	1
12:00– 1:00	6	4	0	2	0	2	0	1
1:00– 2:00	3	1	2	1	0	3	0	1
2:00– 3:00	2	2	1	0	1	1	0	0
3:00– 4:00	0	3	0	1	Cloudy		Cloudy	
4:00– 5:00	3	3	1	0	0	2	0	0
5:00– 6:00	—	—	—	—	1	3	0	0
P.M.								
Total:	34	39	23	27	18	36	10	25

were marked and released within five minutes after their capture. During 1954, it was possible to catch nearly all of the butterflies recorded because they frequented flowers (*Cirsium* spp., *Mertensia ciliata* (James) G.Don., *Oxytropus lambertii* Pursh, *Erysimum asperum* (Nutt.) D.C., and *Penstemon unilateralis* Rydb.) to a much greater extent than they did in 1955, probably because the former summer was much drier. (All Colorado plants were determined by Weber's (1953) handbook.) The records for both years include specimens that were observed as well as caught. This method might have introduced error into the data due to the inadvertent recording of the same specimen more than once per day, but this did not appear to be happening because the recapture of marked specimens indicated that only a low percentage was being recaptured the same day of release. Moreover, there was no differential among the species. In 1955, when most of the records were based on observed specimens, only 9% of 197 of those that were caught were recaptured on the same day. In 1954, this percentage was somewhat higher (16% of 139) but because nearly all individuals were captured it was possible to exclude the error from the data.

The direction of flight of each specimen was recorded in order to find out whether or not there was any mass diurnal reversal in flight direction, and if so whether it was the same in all species, for if it were not the same, individuals of one species could have been recorded twice in one day, while individuals of the other species only once. An analysis of the Utah data in table A suggested that reversal in flight direction is not a general phenomenon. In both *P. rutulus* and *P. multicaudatus,* the number of specimens flying up or down the canyon each hour did not change significantly throughout the day (P greater than .10 in each comparison), although a majority of both species flew down on the second day (P less than .025 for each species).

During 1954, observations were made at the three stations from 28 June to 20 July between 8:00 A.M. and 5:00 P.M. (M.S.T.) or between 8:00 A.M. and cloud cover. On 3 July, the data were collected only between 10:00 and 11:00 A.M. Wherever the butterflies were observed, it was found that their main flight period was in the morning; after 12 noon the

frequency of individuals dwindled and their occurrence became sporadic. Because of this, and because in 1955 it was nearly always clouded in by 1:00 P.M., records for this year were kept only between 8:00 A.M. and 1:00 P.M. During 1955, so few individuals were seen at Station 1 that only observations at Stations 2 and 3 were recorded, and these were often made simultaneously by two sets of observers. The records range from 18 June to 30 July excepting 13 July to 22 July because this time was taken to gather a comparative series of data in Utah.

The Utah data were collected along Big Cottonwood Creek in Salt Lake County. This creek has its headwaters in the Wasatch Mountains near Silver Lake at an altitude of approximately 10,000 feet, and it flows westward into the Great Basin for about 22 miles through a lush, high-walled canyon with numerous tributaries. Observations were made at two stations. The low station was just below the junction of the South Fork of Mill B Creek with Big Cottonwood Creek at approximately 6,300 feet (Station 1). The high station was in the Redman Campground area at an altitude of approximately 8,200 feet (Station 2). Although this canyon is more populated than Left Hand Canyon, it appears to have been less disturbed except in its lower part where the creek is dammed and virtually all of the water is piped to Salt Lake City.

In 1955, collections were made simultaneously at these two Utah stations on 18 July and 19 July from 7:30 A.M. until 5:00 P.M. except at the upper station where observations were curtailed after 12:00 noon on 19 July due to rain. All individuals caught at these two stations in 1955 were kept, and those which were only observed were also recorded as in Colorado. One year later on the same dates, the low station was again visited, but this time no individuals were caught and the data represent only those that

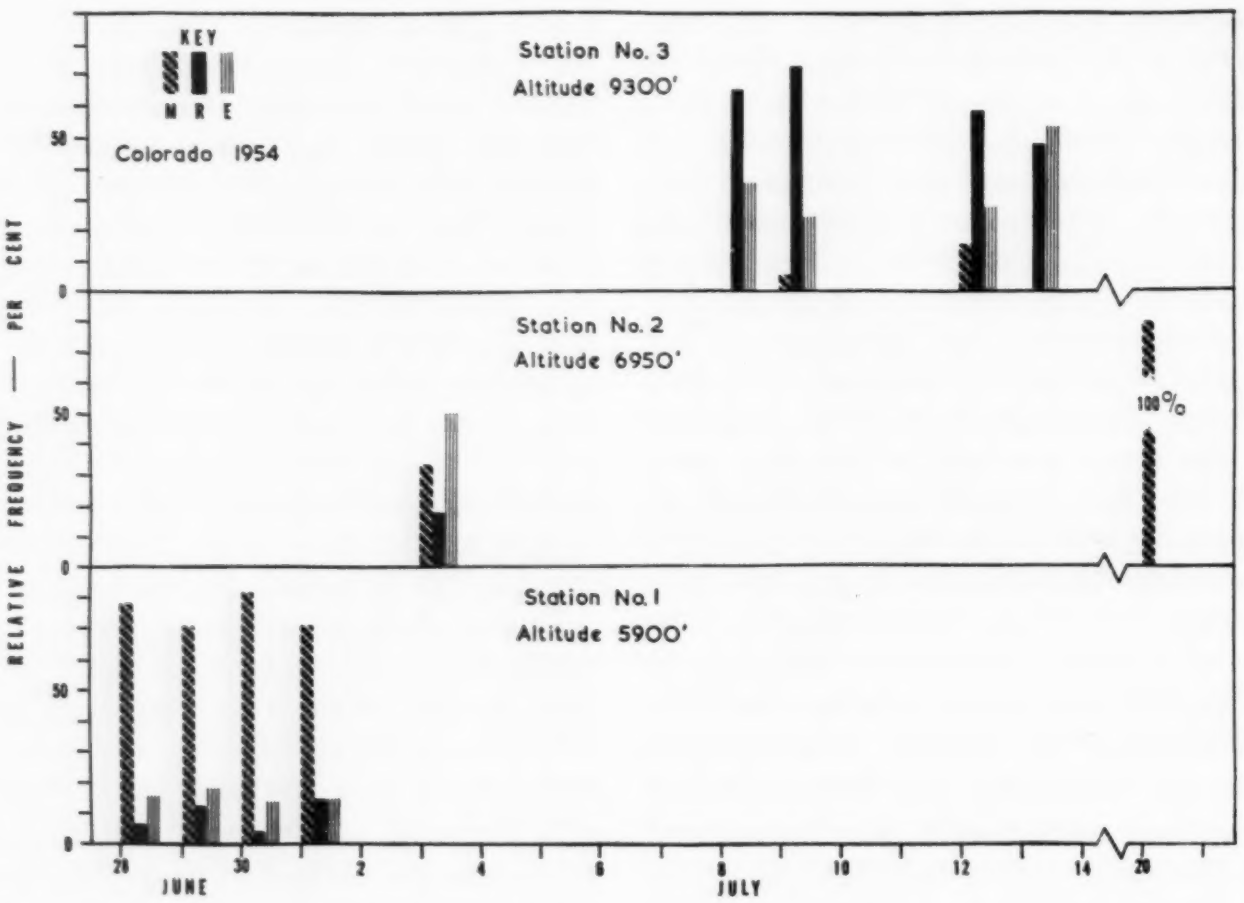

FIG. 1. Relative frequency of *Papilio multicaudatus, P. rutulus,* and *P. eurymedon* at three altitudes in Left Hand Canyon, Boulder County, Colorado, 1954.

were observed. Observations were not made at the high station in 1956.

Most of the individuals seen or caught at the low station in this canyon were flying along the swiftly flowing creek, although a few were netted at *Cirsium* sp. near the roadside about 200 feet north of the creek. The high station was in an area where the creek ran slowly through a relatively wide valley, and the butterflies were far less restricted to the vicinity of the creek than at the low station.

Approximately 4 miles below the low station at Cottonwood Weir (altitude 4,961 feet) and about 1.5 miles above the high station at Brighton (altitude 8,700 feet), the Salt Lake City water department maintains weather stations from which daily records are published in the U. S. Weather Bureau Climatological Data. The monthly mean difference in temperature between the two areas is approximately 20° F. from March to October. For example, at Cottonwood Weir the monthly mean minimum and maximum temperatures for July 1955 were 64° and 93° F., while at Brighton they were 43° and 72° F.

Results of the Ecological Study Colorado 1954

The data collected in Left Hand Canyon, Colorado, during 1954 are presented in table 1 and figure 1. At the lowest and highest stations, the data were gathered at different dates which represented the latter part of the flight periods for all three species in each area. It can be seen that *P. multicaudatus* is more common relative to *P. rutulus* and *P. eurymedon* at the low station, whereas at the highest the reverse is true. The difference between *P. multicaudatus* and either *P. rutulus* or *P. eurymedon* at the two stations is highly significant (P less than .001). A comparison of *P. rutulus* and *P. eurymedon* showed that the proportion of *P. eurymedon* was significantly higher than *P. rutulus* at the low station (P less than .01). Thus *P. eurymedon* appears to be the least restricted in altitude, although it is most similar to *P. rutulus*.

TABLE 1. *Number of individuals of* Papilio multicaudatus, Papilio rutulus, *and* Papilio eurymedon *at Station 1, 2, and 3 in Left Hand Canyon, Boulder Co., Colorado, in 1954*

Station 1 (Altitude 5900′)	Species		
Date	Pm	Pr	Pe
28 June	25	2	5
29 June	24	4	6
30 June	23	1	4
1 July	25	5	5
Totals*	97 (75%)	12 (9%)	20 (16%)
Total M:F	57:25	3:9	5:14

Station 2 (Altitude 6950′)	Species		
Date	Pm	Pr	Pe
3 July	2	1	3
20 July	24	0	0
Totals*	26	1	3
Total M:F	15:5 (20 July only)		

Station 3 (Altitude 9300′)	Species		
Date	Pm	Pr	Pe
8 July	0	24	13
9 July	2	26	9
12 July	7	28	13
13 July	0	9	10
Totals*	9 (6%)	87 (62%)	45 (32%)
Total M:F	6:1	46:24	22:9

* Totals include sexed and unsexed (observed only) individuals.
M = males; F = females.

Two lines of evidence indicate that *P. rutulus* and *P. eurymedon* in general occur at an earlier date in the season than *P. multicaudatus*. The first is based on insufficient data, but is suggested by the presence of all three species at the intermediate station on 3 July, but the absence of both *P. eurymedon* and *P. rutulus* on

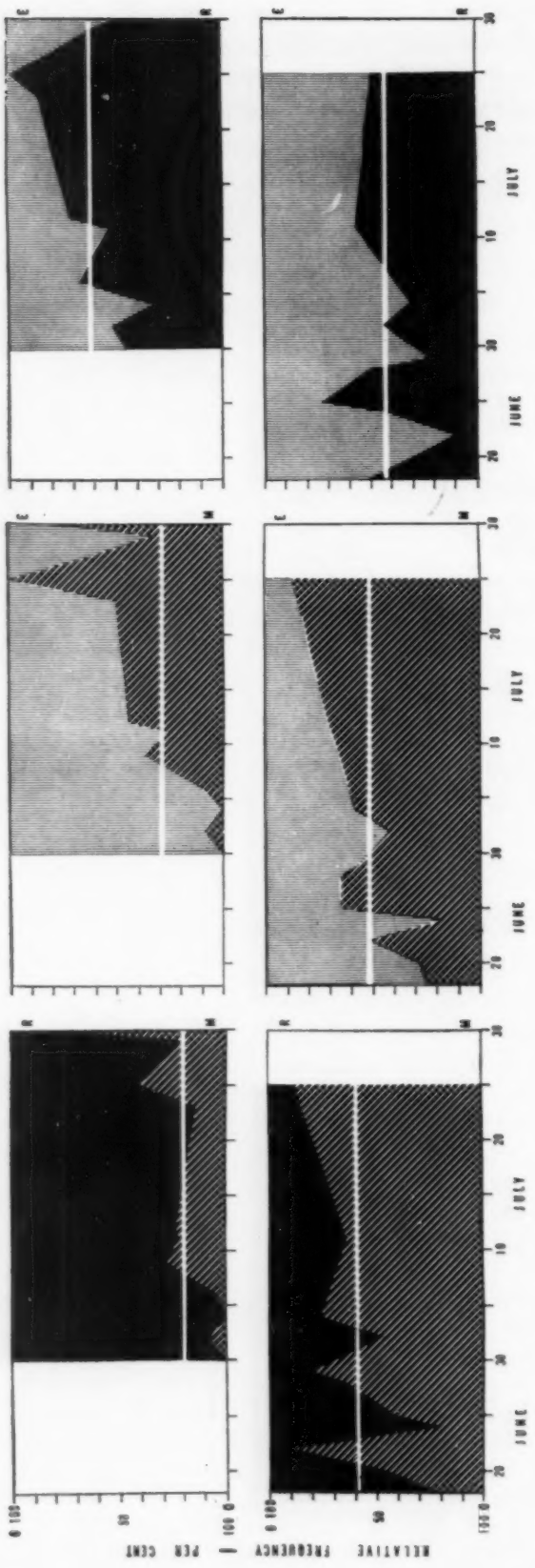

FIG. 2. Relative frequency of pairs of *P. multicaudatus*, *P. rutulus*, and *P. eurymedon* at two altitudes in Left Hand Canyon, Boulder County, Colorado, 1955. Top row: Station 3 (altitude 9,300'), bottom row: Station 2 (altitude 6,950'). Horizontal white lines: mean relative frequency.

20 July. The second line of evidence is the proportion of the sexes of the different species. At the lowest station, females of both *P. eurymedon* and *P. rutulus* outnumbered their males by 3 to 1, while in *P. multicaudatus* the males were more than twice as common as the females. The differences between *P. multicaudatus* and either *P. rutulus* or *P. eurymedon* are highly significant (P less than .001). If two underlying assumptions are valid, then this difference in sex ratio is a strong indication that *P. rutulus* and *P. eurymedon* emerge earlier in the season than *P. multicaudatus*. The first is that if there is any differential habitat preference by one sex, it is the same in all three species. The second is that males eclose before females. This latter assumption appears to be justified for insects in general (Richards, 1927). Scudder (1889) and Sheppard (1953) have discussed the significance of this phenomenon and point out that it is a mechanism to assure that the greatest possible number of females will be fertilized as soon as possible after eclosion.

Colorado 1955

The data in table 2A and figure 2 were collected during 1955 in Left Hand Canyon at Station 2 and Station 3. At Station 2, the data as a whole do not include the initial part of the flight period of all the species, but at Station 3 the greater part of the flight period was covered by the inclusive dates. Figure 2 was constructed to show the mean relative frequency of the species by pairs and to show the change as the season advanced. A comparison of the species at the two stations between 29 June and 25 July indicates that the frequency of *P. multicaudatus* relative to *P. rutulus* or *P. eurymedon* is significantly higher at Station 2 than at Station 3. *P. eurymedon* relative to *P. rutulus* is also more common at Station 2 as compared to Station 3, where *P. rutulus* predominates (P values all less than .001). These data sub-

stantiate the 1954 findings by again indicating that *P. multicaudatus* is the species most restricted to lower altitudes, *P. rutulus* to higher altitudes, and that *P. eurymedon* is on the whole most similar to *P. rutulus* but at the same time less restricted. The similarity of the relative frequencies of the three species at Station 3 during these two summers is noteworthy. In 1955, *P. rutulus* comprised 53%, *P. eurymedon* 33%, and *P. multicaudatus* 14%. In 1954, the respective figures were: 62%, 32%, and 6% (table 1 and table 2A). It would be interesting to know whether the relative frequencies are maintained over a long period of time or whether they fluctuate.

TABLE 2A. *Number of individuals of* Papilio multicaudatus, P. rutulus, *and* P. eurymedon *at Station 2 and Station 3 in Left Hand Canyon, Boulder Co., Colorado, in 1955*

	Station 2 (Altitude 6950′) Species		
Date	Pm	Pr	Pe
18 June	3	10	9
20	8	9	21
22	17	2	16
24	2	7	10
25	17	24	9
28	13	7	7
29	13	3	10
2 July	10	11	14
4	13	4	9
11	7	4	3
25	15	2	2
Totals:	118 (38%)	83 (27%)	110 (35%)

	Station 3 (Altitude 9300′) Species		
Date	Pm	Pr	Pe
30 June	0	5	6
2 July	1	11	10
4	0	8	17
6	1	18	9
9	5	12	8
11	3	10	9
12	8	26	10
23	3	19	3
25	6	9	0
29	2	7	4
30	3	1	1
Totals:	32 (14%)	126 (53%)	77 (33%)

TABLE 2B. *Comparison of frequency of species by pairs early in season (left of median) to late in season (right of median)*

	Station 2 No. of individuals	
Species	Left of median	Right of median
Pm	47.0	71.0
Pr	53.5	29.5
Median individual on 28 June		
Pm	48	70
Pe	66	44
Median individual on 28 June		
Pr	37.5	45.5
Pe	59.0	51.0
Median individual on 25 June		

	Station 3 No. of individuals	
Species	Left of median	Right of median
Pm	10	22
Pr	69	57
Median individual on 11 July		
Pm	6.5	25.5
Pe	48.0	29.0
Median individual on 9 July		
Pr	51.5	74.5
Pe	50.0	27.0
Median individual on 9 July		

It can be seen from figure 2 for both stations that there is a general tendency for *P. multicaudatus* to increase relative to *P. rutulus* or *P. eurymedon* as the season advances. This change with time was tested by the median statistical test for species pairs at each station. This test consisted of arranging the records for both species of a pair in the order in which they were obtained in the field. The median specimen was then determined, and the frequency of each species to the left of the median was compared to the frequency of each to the right and the resulting 2×2 contingency table was

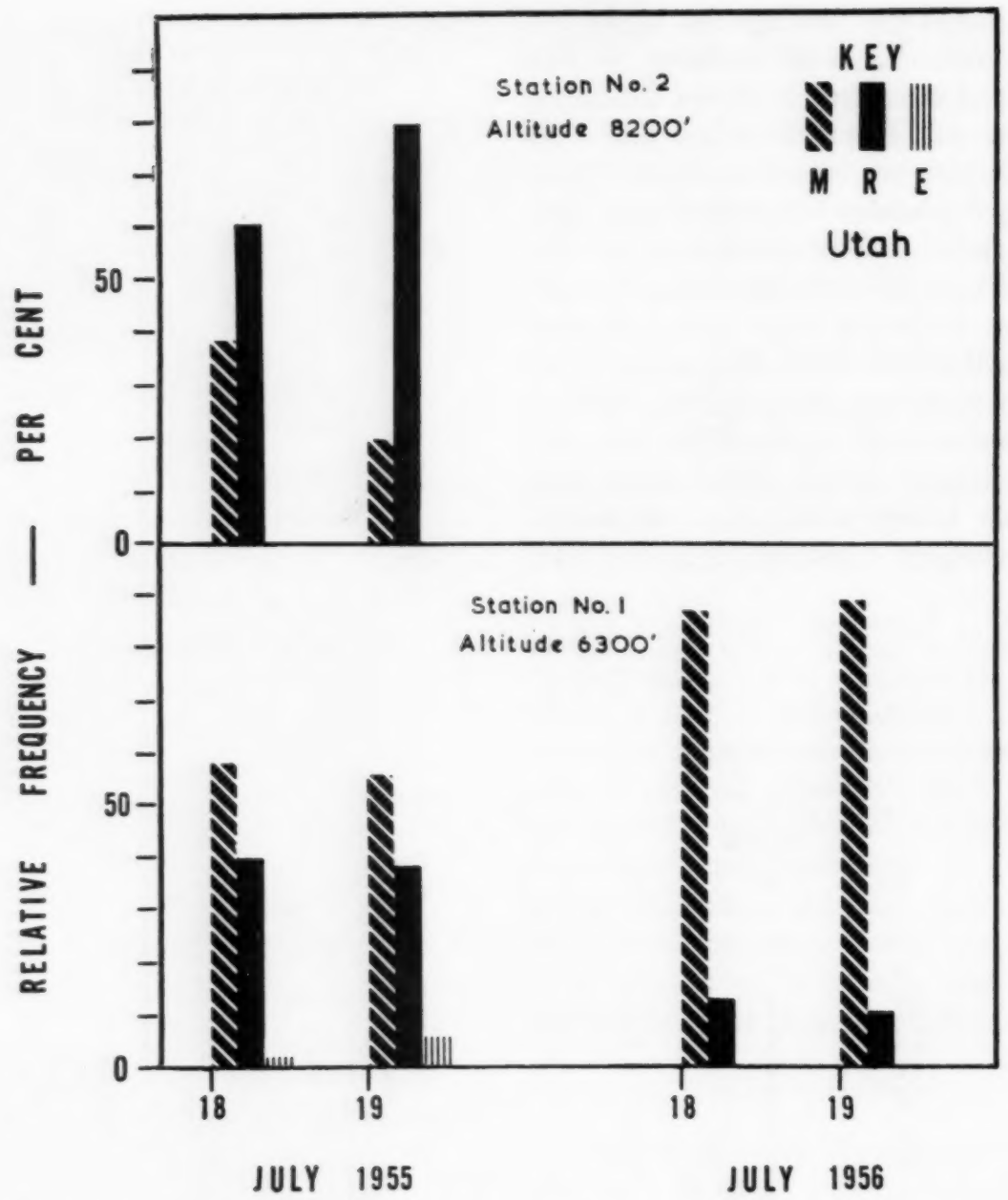

FIG. 3. Relative frequency of *P. multicaudatus, P. rutulus,* and *P. eurymedon* at two altitudes in Big Cottonwood Canyon, Salt Lake County, Utah, 1955 and 1956.

tested by chi-squared. The results of these analyses confirmed that the increase of *P. multicaudatus* relative to *P. rutulus* is significant at both stations (P less than .01 at Station 2; P less than .05 at Station 3). Furthermore, the indication that *P. multicaudatus* was increasing in frequency with time relative to *P. eurymedon* at both was subtantiated (P less than .01 at Station 2; P less than .001 at Station 3). However, at Station 2, neither *P. rutulus* nor *P. eurymedon* was increasing relative to each other (P greater than .10), but at Station 3 the increase in *P. rutulus* is significant (P less than .005). The data for the median tests and the date that the median specimen was collected for each comparison are in table 2B. These results suggest that *P. rutulus* and *P. eurymedon* both have their peak frequency earlier in the season than *P. multicaudatus,* and thus substantiate the 1954 findings.

Utah 1955–1956

The data in table 3 and figure 3 were collected in Big Cottonwood Canyon, Utah. It can at once be seen that the relative frequency of *P. eurymedon* was far less than it had been in the Colorado locality. Although the total number of records for the species obtained at the

TABLE 3. *Number of individuals of* P. multicaudatus, P. rutulus, *and* P. eurymedon *at Station 1 and Station 2 in Big Cottonwood Canyon, Salt Lake County, Utah, in 1955 and 1956*

	Station 1 (Altitude 6300′) Species		
Date	Pm	Pr	Pe
18 July 1955	73	51	2
19 July 1955	55	37	6
Totals	128 (57%)	88 (39%)	8 (4%)
18 July 1956	41	6	0
19 July 1956	32	4	0
Totals	73 (88%)	10 (12%)	0 (0%)

	Station 2 (Altitude 8200′) Species		
Date	Pm	Pr	Pe
18 July 1955	9	14	0
19 July 1955	2	8	0
Totals	11 (33%)	22 (67%)	0 (0%)
18 July 1956	No observations		
19 July 1956			

high station was considerably smaller than at the low station, the frequency of *P. multicaudatus* relative to *P. rutulus* in 1955 was significantly higher at the low station than at the high one (P less than .01). Thus the relative altitudinal distribution of the two species in this Utah locality is similar to that found in the Colorado canyon.

On the same dates in 1956, data were gathered only at the low station in this canyon. In contrast to 1955, *P. multicaudatus* far exceeded *P. rutulus* in numbers (P less than .001), and *P. eurymedon* was not seen at all. The explanation for this difference between the two years is almost certainly that the warm spring of 1956 resulted in an earlier emergence of all the species compared to the emergence in 1955. If this is true, then the preponderance of *P. multicaudatus* relative to *P. rutulus* and the absence of *P. eurymedon* support the hypothesis that *P. rutulus* and *P. eurymedon* emerge earlier in the season than *P. multicaudatus*. Figure 4 is a plot of maximum and minimum temperature differences between these two years four miles below Station 1, and it can be seen that the spring of 1956 was almost continuously warmer than the spring of 1955.

2. Interspecific Sexual Behavior

It has been known for a long time that it is posible to attract wild specimens of the *P. glaucus* group by using caught specimens as decoys (Denton, 1889; Edwards, 1897), and early in the course of the ecological study in Colorado it was observed that dead individuals of both sexes of *P. multicaudatus* and *P. rutulus* placed on thistle blossoms (*Cirsium undulatum* (Nutt.) Spreng) appeared to be indiscriminately courted by males of these two species. It was therefore decided that experiments would be carried out to quantify the courtship of the three western species towards each other and towards the allopatric *P. glaucus*.

The experiments consisted of simultaneously presenting tethered females of two species to wild males of the western species as they flew by in their natural environment. In each experiment, the behavior of a single male was recorded as it courted the females. Simultaneous courtship by males of more than one species was rare either because all the species were infrequent or only one predominated *at the time the experiments were carried out.*

Tinbergen (1948) has pointed out that choice experiments may lead to erroneous conclusions regarding the importance of various elements affecting the courtship

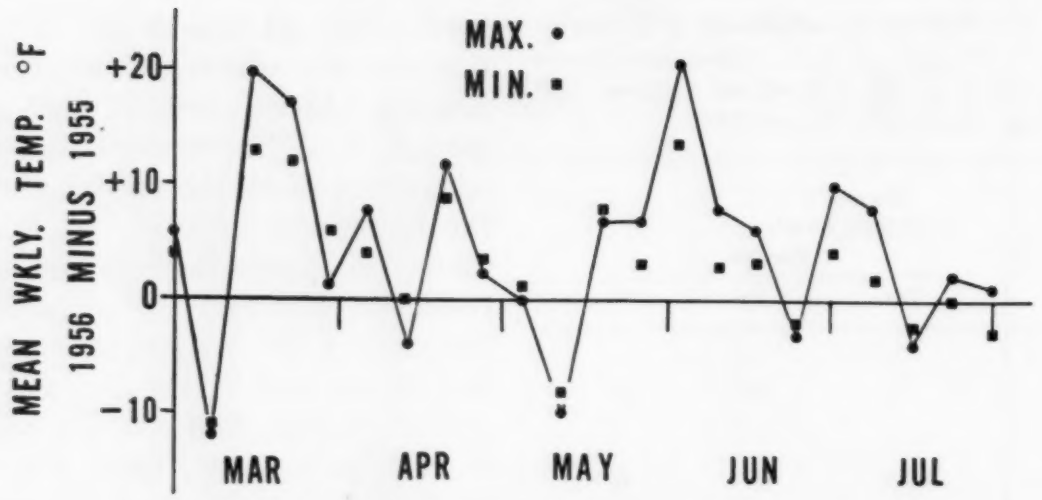

FIG. 4. Temperature differences between 1955 and 1956 four miles below Station 1, Big Cottonwood Canyon, Salt Lake County, Utah. (From U. S. Climatological Data, Cottonwood Weir, altitude 4,961′.)

sequence within a species. This is because "there are two types of sign stimuli, and therefore, two types of releasers: those that direct the response, and those that merely release it without giving spatial guidance. If the latter type is involved, 'choice' experiments are of no use, because one dummy may release the response, while another dummy may be 'chosen'" (p. 146). However, when the purpose is to investigate the courtship between closely related species living in the same area, choice experiments are important for two reasons: (1) if a male of species A releases an undirected courtship response in a female of its own species, a competing male of species B might exploit this response with resultant interspecific copulation; (2) likewise, if male A courts a female of its own species unsuccessfully, it is possible that it might have passed a stage in its courtship sequence which would then allow it to copulate with a female of species B.

The females used in the experiments were secured to a horizontal wire stretched across the creek in the flight path of the wild males. A no. 60 cotton thread was used to "harness" each female butterfly as follows: the thread was first looped around the base of one hindwing, and then continued across the dorsum and looped around the base of the other; the ends of the string which then protruded ventrally from the base of each hindwing were gently drawn together and a knot was tied in the indentation between the third thoracic and first abdominal segments. One end of the thread was clipped short and the other was used to suspend the butterfly from the wire. When a butterfly was tied in this way, it could fly about at the end of the thread. In one case the thread became loose from the wire, and the female flew down canyon in what appeared to be a typical manner. Although the females were restrained by this technique, they were at least able to fly within the bounds determined by the length of the thread. In 1955 it was secured directly to the wire which was not altogether satisfactory because the females tended to circle around the wire. This resulted in shortening the thread so that frequent unwinding was required. Furthermore, there was nothing provided for the females to "perch" on and they often dangled at the end of the thread. In 1956, these difficulties were partly overcome by suspending a sawdust-coated, oval lead sinker 1⅜ in. long from the horizontal wire by means of a 2 foot vertical wire. The female was then tied to the base of the sinker by a 1.5 foot thread. This prevented her circling about the horizontal wire and provided a footing, but some circling about the vertical wire still had to be

remedied periodically by unwinding the thread.

In general the courtship of the males of all three species consisted of fluttering and approaching the female from below, landing on her, attempting to copulate, and in some cases copulating. At any one of these stages the male often flew off for a short distance, circled, and returned; each time a male did this, a single "advance" was recorded. The various categories designated for each male were: (1) the species of female to which it first flew ("female first visited"), (2) the total number of "advances" to each female (minus the single advance towards the female first visited), (3) the number of "attempts to copulate" with each female, (4) whether copulation occurred ("copulations"), and (5) the time spent courting each female. When the data were summarized, another category called "courting males" was added which represents the proportion of males which at some time during their courtship, but not necessarily first, courted the respective females (table 5). Several attempts to copulate during a single prolonged advance period were recorded as one attempt, but if the male circled, returned, and again attempted, another was recorded, *etc*. The time in seconds that each male spent actually courting was recorded with a stopwatch. The time it spent circling was not included in the total because some males did this for several seconds before returning to court.

It was not possible to secure large numbers of pupae for the 1955 experiments, and in 1956 a high pupal mortality occurred. For these reasons the investigation could not be carried out as extensively as had been anticipated and the data include experiments with both virgin and non-virgin females of various ages. It is planned to extend this study using females of uniform age and experience, for as Crane (1957) has found, the courtship pattern of several Trinidad *Heliconius* species changes with time. In fact, there may be a tendency for young virgin *P. multicaudatus* females to copulate faster than older and/or previously mated ones (table 4). The observations did not indicate any obvious differences in the courtship pattern of the males of the western species.

Pupae were obtained for use in 1955 in Colorado as follows: in 1954, I reared *P. multicaudatus* from eggs laid by two females confined in a cheesecloth bag over *Prunus virginiana* in Left Hand Canyon; *P. rutulus* pupae reared in Washington state were purchased from E. Dluhy; *P. glaucus* pupae were also obtained from Dluhy who reared them in Chicago, Illinois, and others were bought from F. T. Naumann who reared them

TABLE 4. *Duration of intraspecific courtship preceding copulation in tethered* P. multicaudatus *females in relation to age and number of previous copulations (Utah 1956)*

	Courtship duration (seconds)				
	Copulation				
Female No.	1st	2nd	3rd	4th	5th
No. 1	0| 8″	4| 55″	—	—	—
No. 2	1| 20″	1| 423″	5| 168″	—	
No. 3	3| 5″	3| 105″	4| 10″	5| 105″	9| 70″
No. 4	3| 238″	4| 434″	—	—	—

Note: Age of female in days in upper left corner.

TABLE 5. *Interspecific courtship in the* Papilio glaucus *group*

Tethered females	Courting males	Female first visited	Advances	Attempts to copulate	Copulations	Total seconds courting
		I. Courtship by 7 *P. rutulus* males (Colorado, 1955)				
P. rutulus	4/7	2	10	2	2	240 (77%)
P. multicaudatus	6/7	5	3	0*	0	70 (23%)
		II. Courtship by 12 *P. multicaudatus* males (Colorado, 1955)				
P. multicaudatus	12/12	10	92	28	4	3914 (84%)
P. rutulus	9/12	2	36	1	0	737 (16%)
		III. Courtship by 35 *P. multicaudatus* males (Utah, 1956)				
P. multicaudatus	25/35	20	63	43	9	4581 (89%)
P. glaucus YEL.	25/35	12	38	6	0*	512 (10%)
P. glaucus BLK.	11/35	3	14	0	0	60 (1%)
		IV. Courtship by 25 *P. multicaudatus* males (Utah, 1956)				
P. multicaudatus	24/25	21	35	17	3	2233 (96%)
P. eurymedon	12/25	4	15	0	0	93 (4%)

P. glaucus YEL. and BLK. refer to the yellow and black female forms of this species.
* See text for further data.

at Forsyth, Georgia. In 1956, *P. multicaudatus* and *P. eurymedon* were hatched from individuals which I found in Left Hand Canyon, Colorado in 1955 on *P. virginiana* and *C. fendleri,* respectively, and *P. rutulus* was obtained from M. W. Osborne who had bought them from Washington state.

After the female butterflies eclosed and expanded their wings, they were separated and placed singly in numbered and dated glassine envelopes. In order to prevent the intermingling of specific odors, the species were kept in separate plastic containers each of which had a slightly moistened piece of paper towel to reduce desiccation. Every evening the butterflies were fed a solution of clover honey and water, after which their legs and proboscises were dipped in water to wash off any residual honey.

Results of the Courtship Experiments

In table 5, the data for all the experiments are summarized in four groups. Group I consists of the courtship of 7 wild *P. rutulus* males with a choice of one *P. rutulus* and one *P. multicaudatus* female. At some time in their courtship, but not necessarily initially, 6 of the 7 males ("courting males") were attracted to the *P. multicaudatus* female, but only 4 were attracted to their own female. The *P. multicaudatus* female was the "female first visited" by 5 of the 7 males. There thus appears to be an initial high response to females of the "wrong" species by *P. rutulus* males. After these first responses, they increasingly directed their attention towards their own species, but on the whole wasted 23% of their time courting *P. multicaudatus.* In addition to these experiments, a *P. rutulus* male in a single similar experiment carried out in Colorado in 1956, first visited the *P. rutulus* female, but immediately left it and courted the *P. multicaudatus* female for 228 seconds. During this courtship, the male assiduously attempted to copulate but failed. It then returned to

its own female, courted it for 32 seconds, and succeeded in copulating after one less prolonged attempt. The inefficiency of the *P. rutulus* male in this case amounted to 88% of its time.

Group II summarizes the courtship by 12 *P. multicaudatus* males when given a choice of one *P. rutulus* and one *P. multicaudatus* female. Unlike the *P. rutulus* males in Group I, all of these males courted their own species and 10 of 12 first visits were to their own female. When the number of advances, the number of attempts to copulate, and the total time courting are compared for the two species of females, inefficiency in the courtship of *P. multicaudatus* is also evident. However, in the experiments of both Group I and II all copulations observed were intraspecific.

In the 35 experiments summarized in Group III, wild *P. multicaudatus* males had a choice of one *P. multicaudatus* female, one black female of *P. glaucus,* and one yellow female of *P. glaucus.* Although the greatest attention of the males was directed towards the female of their own species, they also courted the yellow *P. glaucus* female and even attempted to copulate with it in 6 out of 49 cases. During this time, the black female was practically ignored except for a few advances of short duration. The significant difference (P less than .05) in the attention of the *P. multicaudatus* males towards the black and yellow *P. glaucus* females (in terms of both "courting males" and "female first visited") suggests that the color yellow is important as an initial releaser of courtship behavior in the males of this species. It should be noted that this difference would have been more highly pronounced had the *P. multicaudatus* female not been present. *P. rutulus* males also showed a similar lack of attention towards black *P. glaucus* females in some preliminary experiments carried out in Colorado in 1955.

In Group IV, the courtship of 25 *P. multicaudatus* males is summarized for experiments in which they had a choice of one female of their own species and one female of *P. eurymedon.* It is important to note that the whitish ground color of *P. eurymedon* contrasts with the yellow ground color of both *P. multicaudatus* and *P. rutulus.* The results indicate that the *P. eurymedon* female, like the black *P. glaucus* female, received only cursory notice from less than half of the males. The low proportion of first visits by the *P. multicaudatus* males to the whitish *P. eurymedon* females is highly significant (P less than .005).

Interspecific Copulation Experiments

In one additional experiment (Utah, 1956) a hybrid mating between a yellow *P. glaucus* female and a *P. multicaudatus* male was obtained in the following manner. The male was initially attracted to the yellow *P. glaucus* female which it courted for 20 seconds with one copulation attempt. It then courted the black *P. glaucus* female for 15 seconds, returned to the yellow female for 10 seconds, and flew to the *P. multicaudatus* female. The male courted and attempted to copulate with this female for 35 seconds, circled, returned, and courted the same female for 295 seconds with numerous attempts to copulate. It then circled again, returned to the *P. multicaudatus* female, and courted it for 85 seconds at which point the sinker with the yellow *P. glaucus* female was pushed closer to that of the *P. multicaudatus* female. The yellow female *P. glaucus* fluttered momentarily and the male immediately flew to it, but stayed for only 2 seconds, returning to the *P. multicaudatus* female for 360 seconds. During this time the male vigorously attempted to copulate, but did not succeed. At the end of this period, the male was still with the *P. multicaudatus* female, and the sinker carrying the yellow *P. glaucus* female was drawn even closer to that of the *P. multicaudatus* female, so that the two female butterflies were only about one inch apart. The male now courted the yellow *P. glaucus* female for 5 seconds and succeeded in copulating with it after

only one attempt. Thus, under the conditions of the experiment, interspecific copulation is possible between a male of *P. multicaudatus* and a yellow female of *P. glaucus,* when a *P. multicaudatus* female is also present. In this experiment, the *P. multicaudatus* female had copulated with wild males of its own species on two previous occasions and was five days old. The yellow *P. glaucus* female was virgin, but seven days old, and the black *P. glaucus* female was five days old and virgin.

Another similar experiment was carried out in which I am certain an extended interspecific copulation would have occurred had the yellow *P. glaucus* female been in a more healthy state. In this experiment the *P. multicaudatus* female was removed after it had been courted with several attempts at copulation for a total of 325 seconds during which time the male also courted and attempted to copulate with the yellow *P. glaucus* female. The male then courted the yellow female for a total of 365 seconds, attempted to copulate numerous times, succeeded, but immediately dropped off and continued attempting to copulate. This experiment suggests that the continuous presence of a female of its own species is not necessary for the maintenance of interspecific courtship behavior between a *P. multicaudatus* male and a yellow *P. glaucus* female.

In one experiment, while a *P. multicaudatus* male was courting its own female, the black *P. glaucus* female was similarly pushed adjacent to the courting pair, but this female was not courted by the male. Three other experiments were carried out in which a *P. eurymedon* female was similarly moved close and it also was not courted.

The fact that the *P. multicaudatus* male did court and copulate with the yellow *P. glaucus* female in these experiments, but did not court either the black *P. glaucus* female or the whitish *P. eurymedon* female suggests that the yellow coloration of the female is important for the maintenance of later stages of male courtship behavior. Its importance in initially attracting the males of *P. multicaudatus* has been noted above.

The interspecific courtship between *P. rutulus* and *P. eurymedon* was not investigated, and no attempt was made to obtain eggs from the females used in any of these experiments.

Discussion and Conclusions

The documented larval foodplant records for the members of the *Papilio glaucus* group are summarized in table 6 and it can be seen that *P. glaucus,* which

Table 6. *Summary of documented larval foodplants of the* Papilio glaucus *group.* (+ = suitable, − = unsuitable, 0 = no definite records) *

Foodplant family	*Papilio* species			
	glaucus	*multicaudatus*	*rutulus*	*eurymedon*
Rosaceae	+	+	−	−
Oleaceae	+	+	0	−
Salicaceae	+	0	+	0
Corylaceae	+	0	+	0
Rhamnaceae	0	0	0	+
Magnoliaceae	+	0	−	0
Platanaceae	0	0	+	0
Rutaceae	0	+	0	0
Others	+	0	0	0

The foodplants of *P. alexiares* are unknown.

* From Brower, 1958b.

occurs by itself in eastern and northern North America, has a very generalized foodplant diet. However, the three species which are extensively sympatric and replace *P. glaucus* in western North America are restricted in their diet and feed on mutually exclusive groups of plants. This phenomenon of broad ecological limits in species which occur by themselves in contrast to the restricted ecologies of co-occurring related ones is well known in birds (Lack, 1949, Bourne, 1957), and has been one of the principal indirect arguments that interspecific competition for food takes place in nature. It has been pointed out elsewhere (Brower, 1958) that closely related sympatric insects which are similar in appearance are often found on different foodplants not because food is limiting their numbers, but because the known feeding behavior of some birds is such that the probability of predation of individuals in each of the insect species is increased if they share the same foodplants.

Due to the fact that the larvae of each of the similar western butterflies are on separate plants, such competition between them is precluded. However, as this paper has shown, when the frequencies of adults of the three were studied in a Colorado and a Utah canyon, it was discovered that *P. multicaudatus* is relatively more frequent at lower altitudes and *P. rutulus* at higher altitudes, even though both were present at both altitudes. The evidence also indicated a partial temporal separation of *P. multicaudatus* from the other two which was the result of the maximum emergence of *P. rutulus* and *P. eurymedon* earlier in the season. Although the prevalence of *P. multicaudatus* at lower altitudes and later in the season may in part be an expression of its tendency to include drier and warmer and to exclude wetter and cooler areas in its macrogeographical distribution to a greater extent than is the case for either *P. rutulus* or *P. eurymedon,* this is undoubtedly not the complete explanation because in western California where *P. multicaudatus* is uncommon, *P. rutulus* appears to be less restricted in seasonal occurrence (Brower, ms. in prep.). It is therefore concluded that the partial altitudinal and seasonal separation of *P. rutulus* and *P. multicaudatus* adults in Colorado and Utah is indirect evidence that some competitive relation exists between them.

Elton and Miller (1954) and Hutchinson (1957) have pointed out that there is almost no evidence for the process of competition actually ocurring in nature between species which are at the same trophic level. The former authors defined competition as a situation " in which one species affects the population of another by a process of *interference,* i.e. by reducing the reproductive efficiency or increasing the mortality of its competitor. Or both species may be acting in such a way on each other" (p. 475). The experiments presented in this paper were carried out in the field and indicate that the presence of *P. multicaudatus* and *P. rutulus* in the same area can result in reproductive inefficiency, although gamete wastage through hybridization seems to be very rare (Brower, 1959). From what little is known about butterfly courtship sequences terminating in copulation under natural conditions (Hering, 1926, Carpenter, 1935, Ford, 1945, Portier, 1949), it appears that females are probably mated very soon after they emerge from their pupae. At this time they would be least able to escape from their enemies and it is certain that the presence of a male butterfly persistently and unsuccessfully courting a female of another species would increase the probability of the female being killed by a vertebrate predator. Thus not only is there reproductive inefficiency between *P. multicaudatus* and *P. rutulus* where they occur together, but it is probable that the interspecific courtship increases the mortality of both their females.

By using the laboratory technique of hand pairing different species of *Papilio,* Clarke and Sheppard (1955, 1958) have

reared F_1 hybrids from crosses of *P. rutulus* × *P. glaucus,* and *P. glaucus* × *P. eurymedon,* and it is probable that viable hybrids of any of the western species could be obtained in this manner. In so far as natural hybrids between *P. multicaudatus* and *P. rutulus* are rare, it seems likely that there is some mechanism in the females which inhibits copulation by the wrong males as appears to be the case in many *Drosophila* species (Bastock and Manning, 1955).

One line of evidence from the behavioral study indicates that the interspecific courtship in these two butterflies is due to their similar yellow coloration: the wild *P. multicaudatus* males freely courted and attempted to copulate with experimental females of the yellow form of the sexually dimorphic *P. glaucus,* but almost completely ignored the black females of this allopatric species. The fact that *P. multicaudatus* males also gave very few responses to the *P. eurymedon* females which are whitish in coloration is consistent with this, but here the possibility that olfactory differences may play a role is not ruled out.

The emergence sequence of the two yellow species (*P. rutulus* males, females, *P. multicaudatus* males, females) results in the greatest overlap of *P. multicaudatus* males and *P. rutulus* females and the courtship data, although too limited to be statistically significant, suggest that there is less attraction between these than there is between *P. rutulus* males and *P. multicaudatus females.* It is possible that the relatively poor initial response of the *P. multicaudatus* males towards the *P. rutulus* females is because natural selection has built up a stronger behavioral barrier between these two due to their greater temporal overlap. On the other hand, the fact that *P. rutulus* males were initially attracted to the *P. multicaudatus* females to a greater extent than to their own may be because the larger area of yellow coloration in the *P. multicaudatus* females acts as a supernormal stimulus. Areas of color larger than usual are known to act in this way in two families of butterflies (Satyridae, Tinbergen *et al.,* 1942, Heliconiidae, Crane, 1955), and slight differences in the area of a particular color are known to be very important in the courtship of butterflies in another family (Nymphalidae, Stride, 1955). The solution as to which of these alternative explanations is correct will be found in future experiments by using models.

It is interesting to explore the effect of the relative numbers of the two species on each other as it is probable that the rarer would be at the greater disadvantage. This is because males of the rare one would find females of the common one more frequently than their own. At the same time, the inefficiency of the males of the more common species would be proportionately less because they would more often find their own females than those of the rare species. Moreover, because there are more males in the common species than in the rare one, the amount of predation brought upon the rare female would be proportionately greater than in the common one. In an area where the two are of approximately the same abundance, it is to be expected that *P. rutulus* would sometimes have a greater adverse effect on *P. multicaudatus,* while at other times the relationship would be reversed. This is due both to the fact that oscillations in the numbers of individuals of a population are characteristic of animal species and because it is unlikely that the oscillations will always be in phase (Lack, 1954). If, as the courtship data suggest, *P. rutulus* males are more attracted to *P. multicaudatus* females than the reciprocal, the fluctuation of numbers would probably have the net result of *P. rutulus* males being more inefficient, but *P. multicaudatus* females being more predated.

On the basis of the data presented in this paper, it is suggested that the partial altitudinal and seasonal separations of the two yellow butterflies have been favored by natural selection for their value in re-

ducing the interspecific courtship, and the whitish coloration of *P. eurymedon* has been selected for the same reason. This latter hypothesis is supported by the finding that *P. eurymedon* in Colorado is more widely distributed in altitude than either *P. multicaudatus* or *P. rutulus*.

Although numerous authors have concluded that differences between closely related species have been increased by selection for their value in reducing ecological competition and/or hybridization, these investigations of the *Papilio glaucus* group suggest that partial separations in space and in time may be the result of competition due to interspecific courtship itself. *P. glaucus* and the western species probably also interact in a similar way where they occur together in marginal overlap areas, and this, in addition to the possibility for larval competition between them, may account for their mutual geographic replacement.

Summary

1. This paper is the second in a series on speciation in North American butterflies of the *Papilio glaucus* group.

2. A study of the relative frequencies of adults of the three sympatric western species, *P. eurymedon, P. multicaudatus,* and *P. rutulus,* indicated that two of them (*P. multicaudatus* and *P. rutulus*) are partially separated in altitude in a Colorado and a Utah canyon.

3. A partial seasonal separation of *P. multicaudatus* from the other two was also indicated by a change in relative frequencies as the season advanced, by different sex proportions, and by a comparison of the proportions of individuals of each species present at the same dates for a year with a cool spring and a year with a warm spring.

4. Competition resulting from shared larval foodplants can not have caused the partial temporal and spatial separations because the larvae of each are confined to mutually exclusive groups of plants.

5. In Colorado, the altitudinal preferences do not appear to depend on local foodplant distributions, because foodplants of the separated species are present in abundance at all the altitudes studied.

6. The two species showing the greatest separation are both yellow in coloration, whereas the one which is more generally distributed (*P. eurymedon*) is whitish.

7. A field study of courtship behavior of the butterflies with the use of tethered females indicated that wild males of the two yellow species court and attempt to copulate interspecifically to a greater extent than males of one of these do with females of the white species.

8. Prolonged courtship in two cases resulting in copulation occurred between *P. multicaudatus* males and the similarly colored yellow female of *P. glaucus,* but the black female of *P. glaucus* elicited only few and weak courtship responses from *P. multicaudatus* males.

9. *P. glaucus* probably interacts in its courtship with the two yellow western species where they all occur together in marginal overlap areas and this, in addition to the possibility for larval competition between them, may account for their mutual geographic replacement.

10. It is concluded that the greater tendency for interspecific courtship in the two yellow western species is a possible explanation for their partial separation in space and in time in the two canyons which were investigated. Presumably natural selection has favored altitudinal and seasonal separation as barriers to their interspecific courtship, and the whitish coloration of *P. eurymedon* has been selected for the same reason.

11. This type of selection, which is based on the occurrence of interspecific courtship itself, does not seem to have been emphasized by previous investigators of evolutionary processes.

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Literature Cited

Bastock, M., and A. Manning. 1955. The courtship of *Drosophila melanogaster*. Behavior, **8**: 85–111.

Bourne, W. R. P. 1957. The breeding birds of Bermuda. Ibis, **99**: 94–105.

Brower, L. P. 1958. Bird predation and foodplant specificity in closely related procryptic insects. American Naturalist, **92**: 183–187.

——. 1958b. Larval foodplant specificity in butterflies of the *Papilio glaucus* group. Lepidopterists' News, **12**: 103–114.

——. 1959. Speciation in butterflies of the *Papilio glaucus* group. (1) Morphological relationships and hybridization. Evolution, **13**: 40–63.

Carpenter, G. D. H. 1935. Courtship and allied problems in insects. Transactions of the Society for British Entomology, **2**: 115–135.

Clarke, C. A., and P. M. Sheppard. 1955. The breeding in captivity of the hybrid *Papilio rutulus* female × *Papilio glaucus* male. Lepidopterists' News **9**: 46–48.

——. 1958. The breeding in captivity of the hybrid *Papilio glaucus* female × *Papilio eurymedon* male. Lepidopterists' News, **11**: 201–205.

Climatological Data, Utah. 1955, 1956.. U. S. Department of Commerce, Weather Bureau. Vol. 68–69, Nos. 3–7.

Crane, Jocelyn. 1955. Imaginal behavior of a Trinidad butterfly, *Heliconius erato hydara* Hewitson, with special reference to the social use of color. Zoologica, **40**: 167–196.

——. 1957. Imaginal behavior in butterflies of the Family Heliconiidae: changing social patterns and irrelevant actions. Zoologica, **42**: 135–145.

Denton, S. W. 1889. Catching butterflies by means of decoys. Canadian Entomologist, **21**: 110–113.

Edwards, W. H. 1897. The Butterflies of North America. Third series. Houghton, Mifflin and Co., Boston.

Elton, C. S., and R. S. Miller. 1954. The ecological survey of animal communities: with a practical system of classifying habitats by structural characters. Journal of Ecology, **42**: 460–496.

Ford, E. B. 1945. Butterflies. Collins, London.

Hering, M. 1926. Biologie der Schmetterlinge. Julius Springer, Berlin.

Hutchinson, G. E. 1957. Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology, **22**: 415–427.

Lack, D. 1949. The significance of ecological isolation. In Genetics, Paleontology and Evolution, pp. 299–308, ed. G. L. Jepsen, E. Mayr, and G. G. Simpson, Princeton University Press.

——. 1954. The Natural Regulation of Animal Numbers. Clarendon Press, Oxford.

Portier, P. 1949. La biologie des Lepidopteres. In Encyclopédie Entomologique, ed. P. Lechevalier, Paris.

Richards, O. W. 1927. Sexual selection and allied problems in the insects. Biol. Reviews, **2**: 298–364.

Scudder, S. H. 1889. The Butterflies of the Eastern United States and Canada. 3 vols. Cambridge, Mass. Published by the author.

Sheppard, P. M. 1953. Polymorphism and population studies. Evolution, **7**: 274–289.

Stride, G. O. 1955. On the courtship behavior of *Hypolimnas misippus* L. (Lepidoptera, Nymphalidae), with notes on the mimetic association with *Danaus chrysippus* L. (Lepidoptera, Danaidae). British Journal of Animal Behavior, **4**: 52–68.

Tinbergen, N., B. J. D. Meeuse, L. K. Boerema, and W. W. Varossieau. 1942. Die Balz des Samtfalters. *Eumenis* (= *Satyrus*) *semele* (L.). Zeitschr. fur Tierpsychol. **5**: 182–226.

Tinbergen, N. 1948. Social releasers and the experimental method required for their study. Wilson Bull., **60**: 6–51.

Weber, W. A. 1953. Handbook of Plants of the Colorado Front Range. University of Colorado Press, Boulder.

EVOLUTION IN UPPER JURASSIC AMMONITES

BERNHARD ZIEGLER

Paläontologisches Institut der Universität
Zürich, Switzerland

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Evolution in ammonites has been known for nearly a century. It was mainly under the influence of Charles Darwin (1859) that paleontologists began to look for successions of similar species and to connect these species into lineages. These early studies of evolution in ammonites are due to, e.g., Waagen (1869), Neumayr (1873) and Gemmellaro (1872–82). Before this time most paleontologists did not believe in transformation of species.

All this early work was carried out with scanty material and without a knowledge of the exact stratigraphical location of the species concerned. Nor was there any notion regarding variability in a given species within a stratigraphical unit, i.e., variability of populations. Therefore the lineages set up by these early authors were merely hypothetical.

It was in 1929 that Brinkmann published his study on evolution and variation in the genus *Kosmoceras* in the middle Jurassic of England. Here for the first time transition could be demonstrated from one ammonite species to another, younger one, by careful zonal collecting. Concerning the upper Jurassic, nothing comparable to Brinkmann's study has been published ever since. This is, in part, due to the scarcity of large populations of upper Jurassic ammonites in most countries. Another reason is the great thickness of sediments in other parts of the world. There, because of the slow rate of transformation, a single outcrop is insufficient to show any evolutionary change in the specimens.

As for the upper Jurassic of Southern Germany, it has been possible in the last few years to collect well-preserved material from several horizons of the upper Oxfordian and lower Kimeridgian. In the course of study of the specimens for stratigraphical purposes some interesting observations could be made. The author is deeply indebted to the "Deutsche Forschungsgemeinschaft" for enabling him to execute the work the results of which will now be reported.

CRENICERAS

Creniceras dentatum (Reinecke) is a species very characteristic of the lower Kimeridgian of Southern Germany. It is a small species, measuring about 20 mm. in diameter. In the young *Creniceras dentatum,* the umbilicus is very narrow, becoming much wider abruptly at the transition to the body-chamber. The body-chamber is about two-thirds of a whorl in length. The aperture is marked by lateral lappets. The whorls are smooth except for a row of sharp external teeth. These teeth have their maximum height about half a whorl behind the aperture. Approaching the aperture, the teeth disappear and often a slight external furrow can be observed (for further details regarding *Creniceras,* see Ziegler, 1957).

Comparison of adult specimens of *Creniceras dentatum* shows that specimens from the lowest Kimeridgian (e.g., *tenuilobatus*-zone) are much smaller than specimens found in the upper part of the lower Kimeridgian. 235 specimens, the stratigraphical position of which had been accurately determined, were collected and measured (fig. 1). There is evidence of a remarkable change in size taking place between the *tenuilobatus*-zone and the lower *pseudomutabilis*-zone. Whereas

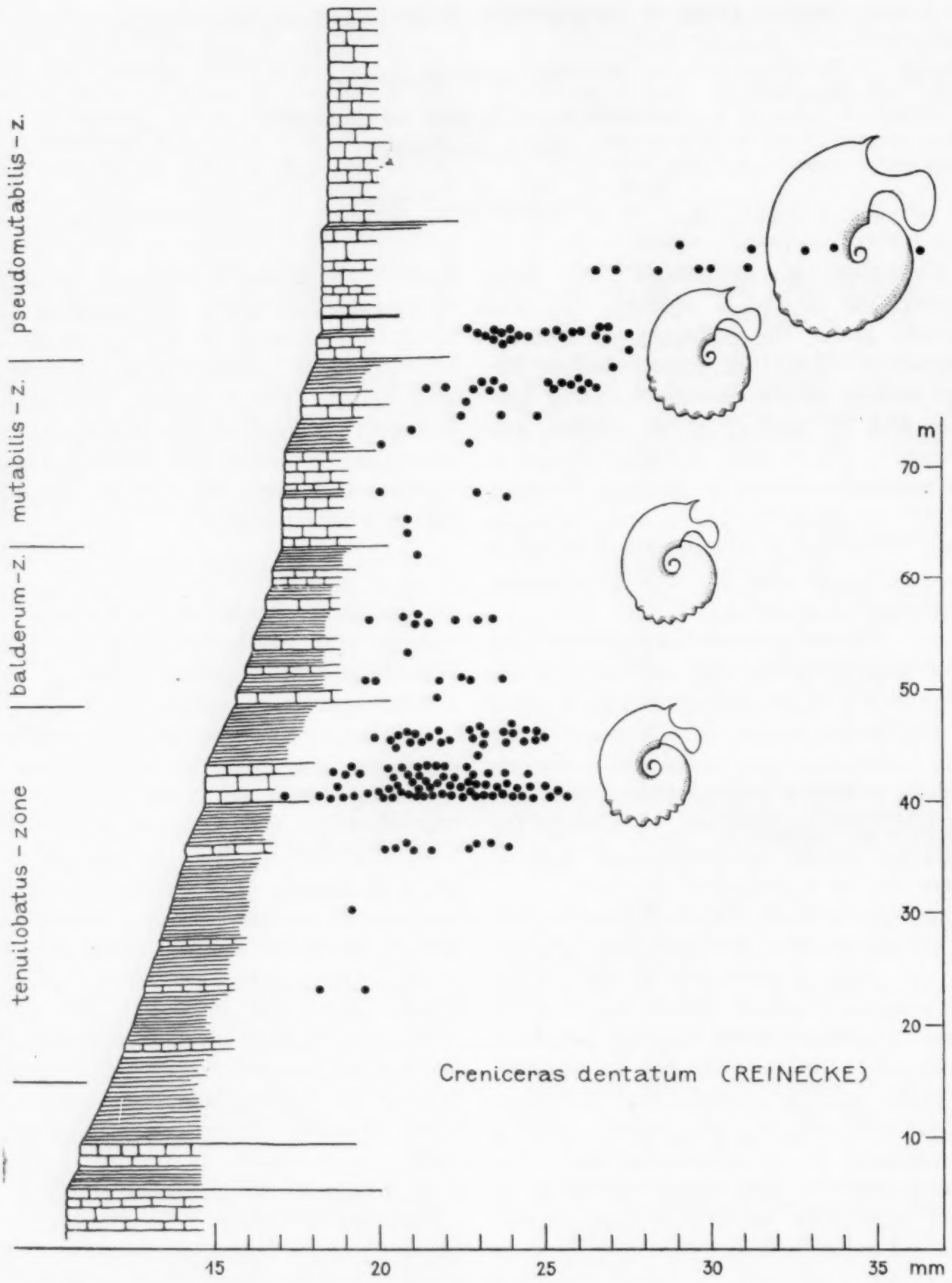

FIG. 1. The diameter of *Creniceras dentatum* (Reinecke) in the lower Kimeridgian of Southern Germany.

specimens from the lower *tenuilobatus*-zone are about 20 mm. in diameter, the stratigraphically youngest specimens known reach a diameter of about 32 mm. This change is arrived at step by step; there is no discontinuity in the evolutionary process.

Apart from a change in overall size, *Creniceras dentatum* shows a marked decrease in width of umbilicus. It is to be

noted that change in size and change in umbilicus width are not correlated. The change in size begins in the lower *mutabilis*-zone, whereas umbilical width remains unchanged until the uppermost *mutabilis*-zone.

A third feature that changes with time is the height of the external teeth. Whereas the oldest individuals bear sharply pronounced teeth, the stratigraphically youngest specimens show but very reduced, small and flat knobs.

The extraordinary stratigraphical range of *Creniceras dentatum* deserves mention. The species occurs through about 70 meters of sediment and through four zones based upon ammonites. One might of course argue that specimens from the lower *pseudomutabilis*-zone, that show a diameter of about 30 mm., a narrow umbilicus and weak teeth, are attributable to a different species than the specimens from the *tenuilobatus*-zone. However, it is definitely impossible to break up this continuously evolving series into "species."

Continuous evolution in ammonites is well known. Brinkmann recognized it in the famous genus *Kosmoceras,* and recently Callomon (1955) has confirmed Brinkmann's findings. An investigation of the upper Jurassic genus *Taramelliceras* (Hölder, 1955) reveals an analogous situation.

Although it is believed that the evolution of ammonites is subject to inherent trends, we must not exclude the possibility that additional factors of an external nature might be involved. It is very striking that, during the time that *Creniceras dentatum* underwent its progressive size increase, the area of sponge reefs in the upper Jurassic ocean of Southern Germany was spreading out rapidly. It is tempting to assume that the expanding sponge reefs had an influence upon the feeding conditions of *Creniceras*. In this case the change in size may not have been genetically determined but merely a response to environmental conditions.

In order to test the influence of sponge reefs, samples of *Creniceras dentatum* were collected from several different but contemporaneous biotopes. Specimens were collected at the following sites: within a large sponge reef; far out from the reefs; and near the border of little reefs, the so-called "Schwamm-Stotzen." In all of the samples collected the same variability in size and the same maximum frequency of diameter (of about 22 mm.) were found. It seems therefore that the spreading sponge reefs had nothing to do with the size increase of *Creniceras dentatum.*

Another external factor possibly influencing size could have been the percentage of $CaCO_3$ present in the sediment. Indeed, the small specimens of the *tenuilobatus*-zone are chiefly found in more marly sediments; the large specimens of the lower *pseudomutabilis*-zone chiefly in limestones. But we find periods of dominance of limestone as early as the *tenuilobatus*-zone, and also times of dominating marly sedimentation in the uppermost *mutabilis*-zone. If the size of *Creniceras dentatum* were influenced by the percentage of $CaCO_3$, all these periods of altered sedimentation should also show this effect. This, however, does not seem to be the case.

We must thus say that the sediments involved give no clues concerning the change of size in *Creniceras dentatum,* and therefore conclude that inherent trends are responsible for the transformation of *Creniceras dentatum.*' We are completely ignorant as to the basis for these trends.

Not only do the morphological features of *Creniceras dentatum* change in the course of time, but its ecological behavior also changes. It was Engel (1908) who first noted that *Creniceras dentatum* lived in close association with little sponge reefs in the *tenuilobatus*-zone. The species is much more abundant close to the reefs than farther out. The situation is entirely different in the *mutabilis*- and lower *pseu-*

domutabilis-zones: here no specimens at all have been found within the little sponge reefs.

SUTNERIA

Most of the famous lineages in paleontology show continuous evolution without a break and without saltation. One of the very rare examples of discontinuous evolution is the genus *Sutneria* in the lower Kimeridgian of Southern Germany.

Sutneria cyclodorsata (Moesch) ranges from the lowest *tenuilobatus*-zone up to the lower *pseudomutabilis*-zone. The species is always rather rare. It is of small size, with rounded whorls and fine, triplicate or quadriplicate, rursi-radiate ribbing. However, at the base of the upper *pseudomutabilis*-zone, *Sutneria cyclodorsata* suddenly disappears and is replaced by the related *Sutneria eumela* (D'Orbigny), a form characterized by coarse duplicate ribbing (fig. 2).

That evolution in this case has been explosive cannot be proven, but it seems very likely that speed of evolution had strongly increased for a short time until the new species was established. In the strata there is no indication of discontinuous sedimentation. Other ammonites, e.g., the genera *Taramelliceras* and *Glochiceras,* cross the boundary between the lower and the upper *pseudomutabilis*-zone without saltation.

There is, of course, a possibility of migration of ammonites. *Sutneria eumela* is found in Southern Germany, in the Paris basin and the Rhône valley. The stratigraphical position of the species has been studied in Southern Germany, as well as in the Rhône valley. In both areas the replacement of *Sutneria cyclo-*

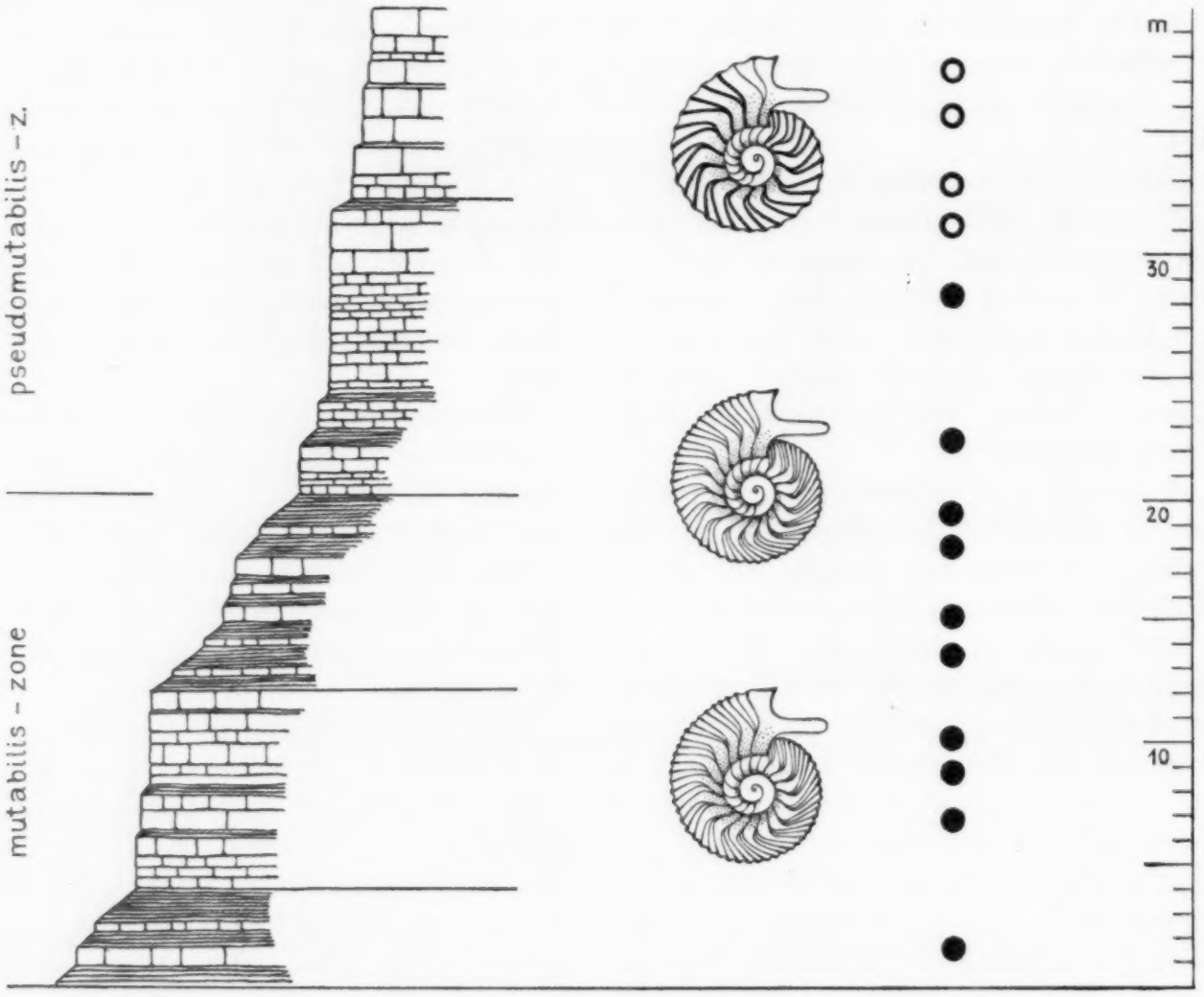

FIG. 2. The transformation from *Sutneria cyclodorsata* (Moesch) (below, black disks) to *Sutneria eumela* (D'Orbigny) (above, black rings) in the lower Kimeridgian of Southern Germany.

dorsata by *Sutneria eumela* takes place simultaneously, as shown by the accompanying ammonite faunas.

Migration of *Sutneria eumela* might have started from the Paris basin since it is very unlikely that the species also occurred in other regions. In the Paris basin, *Sutneria eumela* lived in association with perisphinctids of the genus *Aulacostephanus* which are found also in Southern Germany in the upper *pseudomutabilis*-zone.

There can hardly be any doubt that *Sutneria eumela* evolved from *Sutneria cyclodorsata*. *Sutneria cyclodorsata* is, however, not found in the Paris basin. It therefore seems more likely that *Sutneria eumela* migrated into the Paris basin than the reverse. We are left with the only possible explanation that *Sutneria cyclodorsata* was transformed into *Sutneria eumela* in a burst of accelerated evolution.

The transformation of *Sutneria cyclodorsata* into *Sutneria eumela* is not the only case of rapid evolution in the genus *Sutneria*. Near the boundary between upper Oxfordian and lower Kimeridgian, *Sutneria galar* (Oppel) is a common species. This species gives place suddenly to the related *Sutneria platynota* (Reinecke). There is no doubt that *Sutneria platynota* has evolved from *Sutneria galar*. However, as Dieterich (1940) points out, specimens intermediate between the two species are very rare.

It is likely that just about where *Sutneria platynota* sets in, the beds are somewhat condensed. Therefore, we have no definite proof for a sudden step in the evolution of *Sutneria*, leading to a new species. It is, however, remarkable that other genera, such as *Physodoceras*, *Amoeboceras* or *Glochiceras*, continue to range through the condensed beds without change.

In the middle Kimeridgian, *Sutneria subeumela* Schneid is a species very characteristic of Southern Germany. The species has apparently evolved from *Sutneria eumela* and there is a good deal of evidence pointing to a relatively sudden change in shape.

To summarize, we may say that during the lower Kimeridgian the genus *Sutneria* was submitted to long periods of immutability of species alternating with short periods of highly accelerated evolution. For the periods of species constancy we may use Schindewolf's (1950) term "Typostase"; the phases of highly accelerated evolution we may term "Typogenese."

GLOCHICERAS

A recent study of the genus *Glochiceras* (Ziegler, 1958) reveals additional details of ammonite evolution. The genus *Glochiceras* comprises small, mostly smooth-shelled species. The aperture bears lateral lappets. One of its subgenera, *Glochiceras* s.str., is characterized by a short external rostrum which is separated from the body-chamber by a slight furrow. This subgenus is represented by several species ranging from the beginning of the upper Oxfordian (*transversarium*-zone) to the middle Kimeridgian (*Gravesia* zones).

The species of the subgenus may be arranged in a single lineage; here we may neglect the few additional species that do not fit in this series. The first species is *Glochiceras subclausum* (Oppel) from the *transversarium*-zone. The mean diameter of adult specimens is 30 (22–43) mm. The body-chamber comprises ⅔ of the last whorl. The aperture is more or less rectangular in cross-section. The sutures are clearly denticulate.

In the *hypselum*-zone *Glochiceras subclausum* is very rare. As late as in the *bimammatum*-zone glochiceratids become frequent again. But now they show a mean diameter of 24 (18–28) mm. and the body-chamber amounts to about ¾ of the last whorl. The cross-section near the aperture is still somewhat rectangular but tends to become lenticular. The sutures are denticulate but simpler than in *Glochiceras subclausum*. This species is named *Glochiceras tectum*.

During the *planula*-zone glochiceratids once more are very rare. When they again become frequent in the *tenuilobatus*-zone, they are named *Glochiceras nimbatum* (Oppel). Their mean diameter is 17 (14–20) mm., their body-chamber measures about 7/8 of the last whorl, and the cross-section is lenticular. The sutures are simple, not denticulate. This species does not change remarkably up to the end of the *pseudomutabilis*-zone. In the upper parts of this zone and in the lower *subeumela*-zone glochiceratids again become very rare.

In the *setatus*-zone the evolution of *Glochiceras* assumes an explosive nature. Glochiceratids have become very common. They are again of larger size, their body-chamber becomes shorter and the sutures are clearly denticulate (fig. 3). Owing to the great variability of all morphological characters, it is now very difficult to distinguish the various species (*Glochiceras lens, Gl. lens rostratum, Gl. politulum*). In all these features, the glochiceratids of this period have come to resemble the upper Oxfordian species (fig. 4). The single character permitting separation is the cross-section. Whereas overall size, length of body-chamber and denticulation of sutures are just the same as in Oxfordian species, the cross-section remains lenticular. Since glochiceratids become extinct with these species, Schindewolf's term "Typolyse" is applicable to this phase of explosive evolution in the middle Kimeridgian.

It should be stressed that small size is correlated with a long body-chamber and simple sutures, whereas large size goes together with a short body-chamber and denticulate sutures. If these features alone are considered, *Glochiceras* appears to show definite reversibility of evolution. But if we consider the cross-section, which definitely does change (as also do

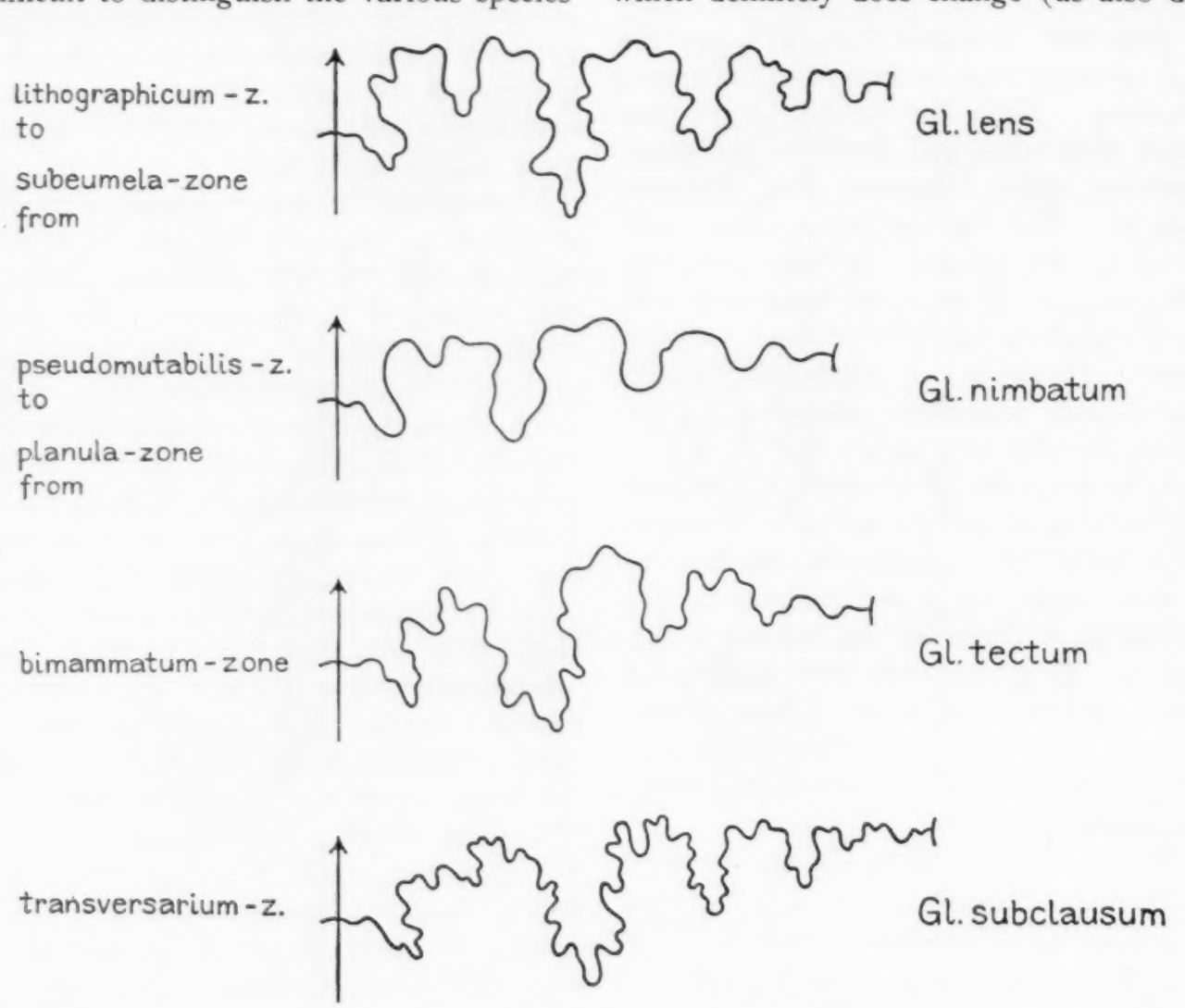

FIG. 3. The sutures of some glochiceratids from the upper Oxfordian (below) to the middle Kimeridgian (above).

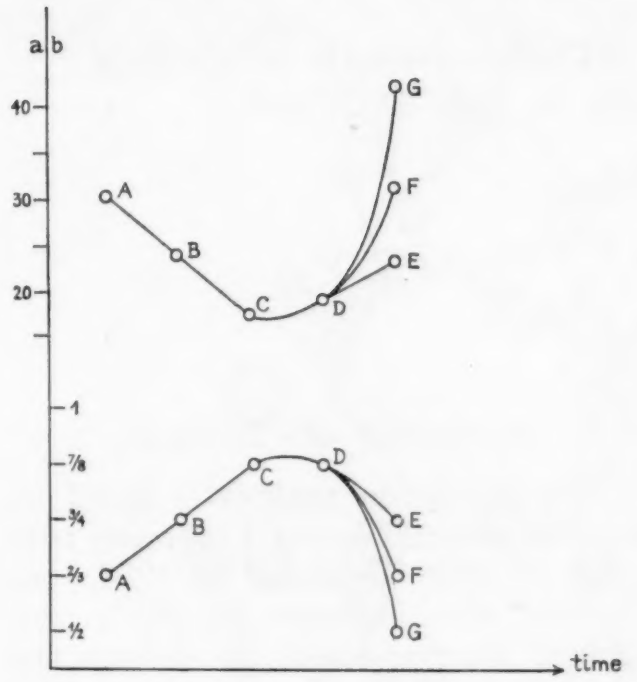

FIG. 4. The diameter (a, in mm.) and the length of body-chamber (b) in the species of the genus *Glochiceras* from the upper Oxfordian (on the left) to the middle Kimeridgian (on the right). A: *Glochiceras subclausum* (Oppel); B: *Glochiceras tectum* Ziegler; C, D: *Glochiceras nimbatum* (Oppel); E: *Glochiceras lens lens* Berckhemer; F: *Glochiceras lens rostratum* Berckhemer; G: *Glochiceras polituluum* (Quenstedt).

other characters), we find that *Glochiceras* is an example of irreversible evolution.

As already mentioned, glochiceratids are very rare during the periods in which its species were being recast. The cause for this scarcity can hardly be sought in general environmental factors, since other species and genera retain their abundance during these periods. Neither can we assume a migration of new forms from elsewhere since we have to regard the upper Jurassic ocean of Southern Germany as the evolutionary centre of *Glochiceras*. We are thus forced to consider that rareness of glochiceratids during the periods of speciation is a primary character.

In large populations, new mutations are not likely to penetrate since they tend to be swamped. In small populations, on the other hand, the chance for a new mutation to survive and spread is much greater. The new mutations will, however, lead to a new species only if it is preadapted to any of the ecological niches available.

CONCLUSIONS

We may conclude that in ammonites evolution is mostly continuous. In a very few cases, however, discontinuous evolution at the species level, brought about by temporarily accelerated evolution, is highly probable. Such accelerated development leading to discontinuity in evolution seems to be restricted to small populations where new mutations have a better chance to spread.

LITERATURE CITED

BRINKMANN, R. 1929. Statistisch-Biostratigraphische Untersuchungen an mitteljurassischen Ammoniten über Artbegriff und Stammesentwicklung. Abh. Ges. d. Wiss. Göttingen, Math. phys. Klasse, N.F., **13**, 3. Berlin.

CALLOMON, J. H. 1955. The ammonite succession in the lower Oxford Clay and Kellaway Beds at Kidlington, Oxfordshire, and the zones of the Callovian stage. Phil. Trans. Roy. Soc. London, Ser. B, Biol. Sci., **239**: 215–264, London.

DARWIN, C. 1859. On the origin of species by means of natural selection, or the preservation of favored races in the struggle for life. London.

DIETERICH, E. 1940. Stratigraphie und Ammonitenfauna des Weissen Jura Beta in Württemberg. Jh. Ver. vaterl. Naturkde. Württ., **96**: 1–40, Stuttgart.

ENGEL, TH. 1908. Geognostischer Wegweiser durch Württemberg. Stuttgart. 3d ed.

GEMMELLARO, G. 1872–82. Sopra alcune faune giuresi e liasiche della Sicilia. Palermo.

HÖLDER, H. 1955. Die Ammonitengattung *Taramelliceras* im südwestdeutschen Unter- und Mittelmalm. Palaeontographica, **106A**: 37–153. Stuttgart.

NEUMAYR, M. 1873. Die Fauna der Schichten mit *Aspidoceras acanthicum*. Abh. k. k. geol. R. A., **5**: 141–257. Wien.

SCHINDEWOLF, O. H. 1950. Grundfragen der Paläontologie. Stuttgart.

WAAGEN, W. 1869. Die Formenreihe des *Ammonites subradiatus*. Beneckes geognost.-paläont. Beiträge, 2, München.

ZIEGLER, B. 1957. *Creniceras dentatum* [Ammonitacea] im Mittel-Malm Südwestdeutschlands. Neues Jb. Geol. Paläontol., Mh. 1956: 553–575. Stuttgart.

——. 1958. Monographie der Ammonitengattung *Glochiceras im* epikontinentalen Weissjura Mitteluropas. Palaeontographica, **110**: 93–164.

POPULATION ANALYSIS OF A HYBRID SWARM BETWEEN *GAMBUSIA AFFINIS* AND *G. HETEROCHIR*

CLARK HUBBS

The University of Texas

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INTRODUCTION

Many natural fish hybrids have been reported by Carl L. Hubbs (1955). Most of the known hybrid combinations are based on few specimens. Some localities are known where hybrid frequency is high enough to be considered to represent a hybrid swarm. An analysis of the population of one such hybrid swarm is presented below.

This hybrid swarm and degree of parental relation was reported in a previous paper (Hubbs, 1957a). One parental species, *G. heterochir* Hubbs, is restricted to the hybrid area in Clear Creek, Menard County, Texas. Its abundance is correlated with the distribution of a species of *Ceratophyllum* and the distribution of this plant is correlated with the relatively low water pH there. The low pH in turn is probably dependent upon Permian inliers in Cretaceous strata (Hubbs, 1957b).

The other parental species, *G. affinis* (Baird and Girard), is widely distributed in the southeastern United States where it occupies a variety of habitats. In Texas and northern Mexico it is notably absent from clear spring waters inhabited by other gambusiine fishes. However, it occupies this habitat in the absence of related species. In some spring localities (i.e., in Graham Ranch Warm Springs in Brewster County, Texas) *G. affinis* is replacing endemic stocks of *G. gaigei* Hubbs and in others *G. affinis* is being replaced by introduced stocks of *G. geiseri* Hubbs and Hubbs (Hubbs and Springer, 1957).

MATERIALS AND METHODS

This population analysis is based on material obtained during 4 collecting trips (July 16, 1956, December 16, 1956, June 15, 1957, and November 29, 1957). Additional observations of the ecology and population structure were made on May 31, 1958. Specimens from 16 localities (A–P on fig. 1) in and around the hybrid area are analyzed. The localities are all in the impounded part of Clear Creek. Four are above the upper dam and 12 below. All collections are within an area about 300 yards square.

Because of extreme dimorphism the sexes are treated separately. Three dimensional plots were made following techniques given by Anderson (1949) as well as two dimensional plots slightly modified from techniques given by Hubbs, Hubbs, and Johnson (1943). Although Anderson's technique shows more detail, it is not presented here to save space and make interpopulation comparison easier.

Four main characters are used for each female. The number of dorsal rays have been counted (all counts and measurements follow Hubbs and Lagler, 1947). In coding, each dorsal ray is allocated two units. Thereby the modal number of 6 dorsal rays for *G. affinis* is given a value of 12 and the modal number of 8 for *G. heterochir* is valued at 16. The number of pectoral rays has been counted. Similar to dorsal ray counts, each pectoral ray is valued at 2 units. Thereby the modal number of 13 for *G. affinis* is allocated a value of 26 and the modal number of 15 for *G. heterochir* is valued at 30. The relative bulk of the head is

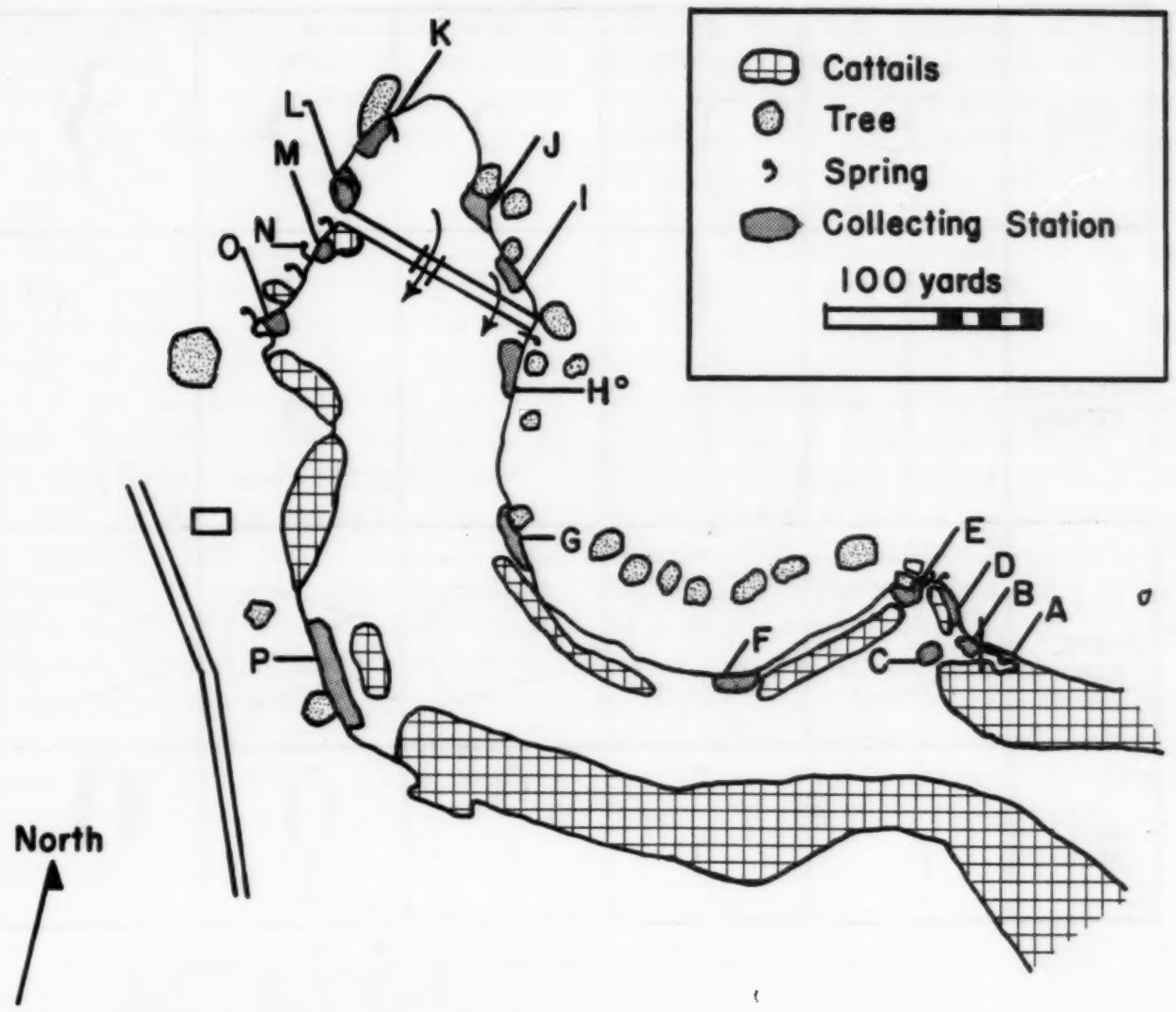

FIG. 1. Map of station localities. Arrows show direction of water flow over the spillway and through a break in the dam. Between November 29, 1957, and May 21, 1958, the cattails were virtually eradicated from this region by nutria, *Myocaster coypus* (Molina), which had been introduced previously.

determined by adding the head width and depth at the rear of the orbits. The figure is divided by the standard length. The absolute per cent (not rounded) is used in coding. Modal figures are near 33 for *G. affinis* and near 38 for *G. heterochir*. The relative head bulk decreases with size increase. Thereby only adult females 25 mm. standard length or longer are used. Nevertheless, some variation with size is apparent in these figures. Four color characters are used: extent of scale crescents on sides; extent of anal spots; strength of predorsal streak; and strength of caudal bar. The codings for these color marks are given in figure 2. Modal numbers for *G. affinis* are near 7 and are near 16 for *G. heterochir*. Color characters tend to vary due to two non-genetic factors. Fish from light environments have less developed color marks than those from dark habitats. Young fish have less developed color marks than old fish. Two of the color marks used are best developed in *G. affinis* and the other two in *G. heterochir*. Thereby a *G. heterochir* with weakly developed colors might be coded low in *G. heterochir* color characters; however, she would totally lack *G. affinis* color marks and thus be coded high for those pattern attributes. This would lower the effect of non-genetic color pattern factors. The coded figures for each female are totaled. Modal values are 77 and 99 for *G. affinis* and *G. heterochir* respectively.

Five main characters are used for each male. Only males with the gonopodial

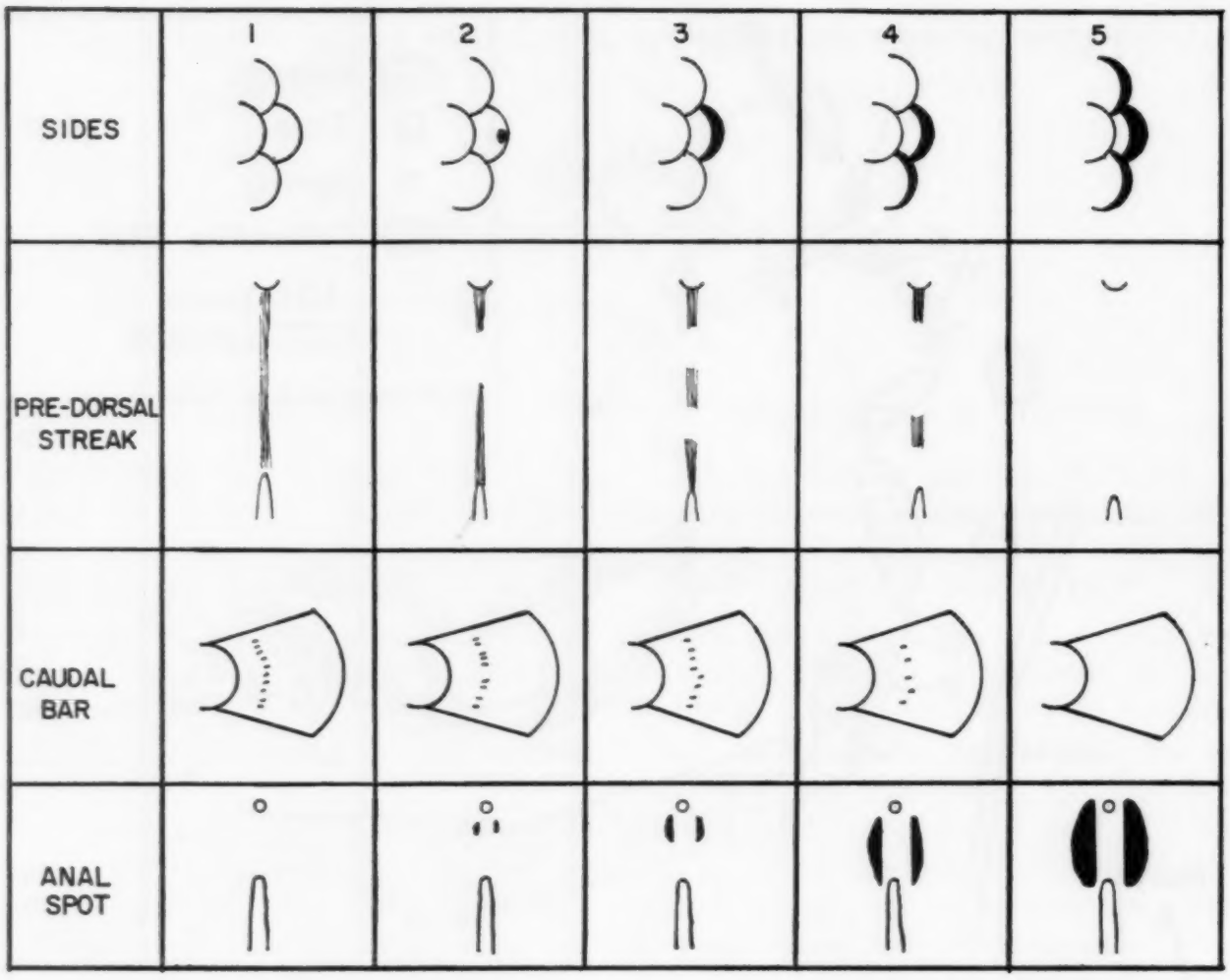

FIG. 2. Color codings for females. (Redrawn from figure 4 of Hubbs, 1957a.)

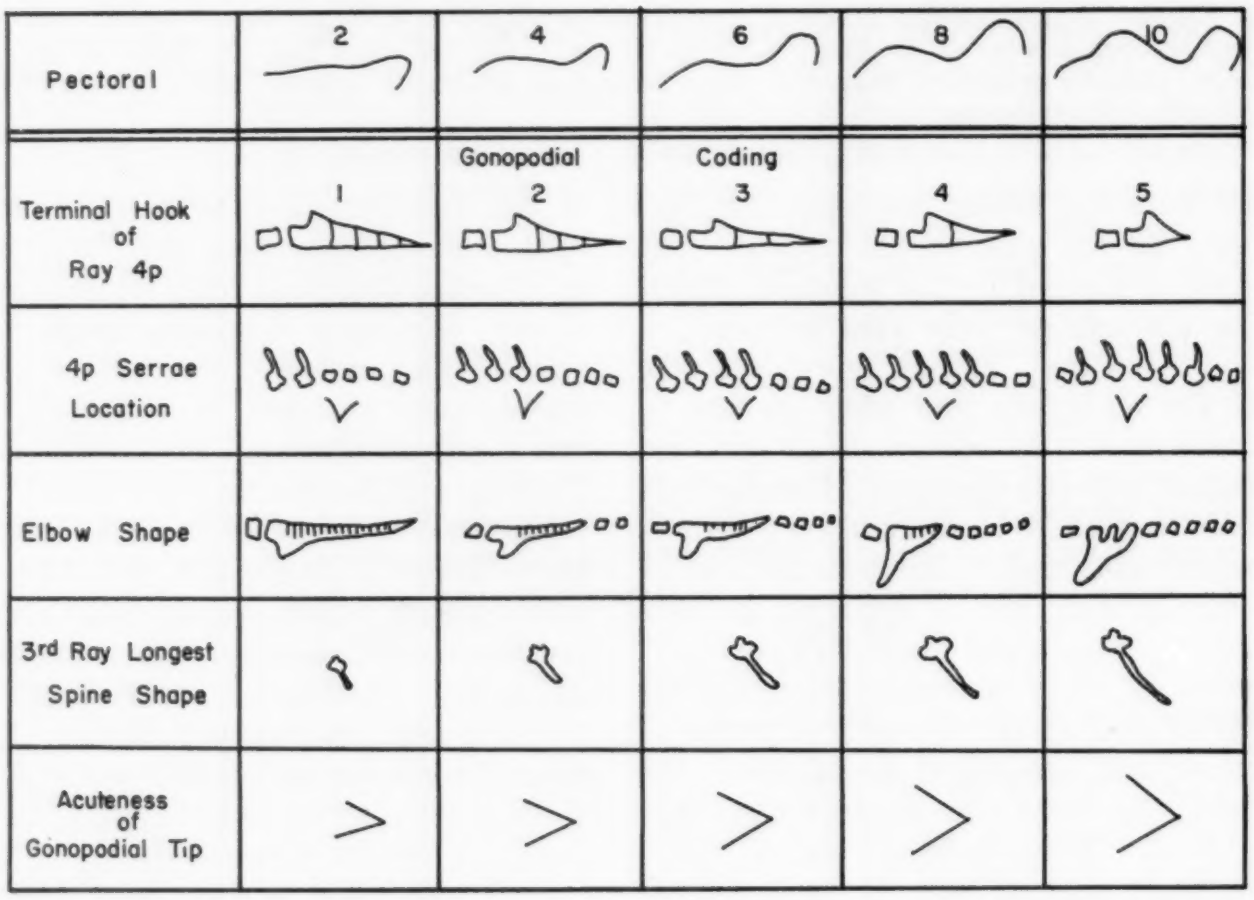

FIG. 3. Codings for pectoral fin shape and gonopodial structures of mature males.

tip clear are used to reduce effects of age variation. Pectoral ray numbers correspond to those for females, but because of the difficulty of accurate counts on small males this character is not used in the plots. Dorsal fin ray numbers are coded as in females. The head porportions are coded as in females; however, due to sexual dimorphism the modal figures for *G. affinis* are 30 and the modal figures for *G. heterochir* are 36. As mature gambusine males have terminal growth (Hubbs and Springer, 1957), influence of size on males is less than on females. Two color characters are used: extent of scale crescents on sides, and strength of the predorsal streak. These are coded as in females and affected by the same non-genetic factors; however, male terminal growth reduces the magnitude of size effects. The shape of the upper margin of the pectoral fin is coded as shown in figure 3. The modal figure for *G. affinis* is 2 and that for *G. heterochir* is 10. Five gonopodial characters are used (see Hubbs and Springer for gonopodial nomenclature): the number of segments in the terminal hook of ray 4p; the relative location of the serrae on ray 4p and the elbow on ray 4a; the shape of the elbow; the relative shape of the longest modified spine on ray 3; and the sharpness of the gonopodial tip. The coding of these characters is given in figure 3. Modal numbers for *G. affinis* vary between 6 and 7 while those for *G. heterochir* are between 24 and 25. The coded figures for each male are totaled. Modal values are 54 and 93 for *G. affinis* and *G. heterochir* respectively.

Figures for males are considered more reliable than those for females because of the added coded characters and the reduced effect of allometric growth.

TABLE 1. *Ecologic data on Clear Creek Stations*

Station	Water depth in inches	Surface water temperature, ° C.	pH	Vegetation
A	0–6	15.5–29.0	6.6–7.0	Heavy *Ludwigia* on first visit Sparse emergent vegetation on other visits
B	0–24	19.7–27.0	6.6–6.8	Heavy *Ceratophyllum* on first visit Heavy *Myriophyllum* on second and third visits Mixed *Ceratophyllum* and *Myriophyllum* on last visits
C	24–36	19.7–22.2	6.7	Heavy *Potamogeton*, *Ceratophyllum*, *Hydrocotyl*, and *Jussiaea*
D	0–8	20.0–22.2	6.5–6.6	Sparse *Potamogeton*, *Ceratophyllum*, *Hydrocotyl*, and *Jussiaea*
E	0–36	18.2–28.5	6.8–7.2	Filamentous algae (west of willow tree)
		20.5–21.0	6.4–6.7	Filamentous algae (at spring east of willow tree)
F	0–12	19.1–33.8	6.9–7.6	*Myriophyllum*
G	0–12	17.8–27.5	7.0–7.4	*Myriophyllum*
H	0–24	19.9–31.2	6.8–7.3	*Myriophyllum* and *Potamogeton*
I	0–12	20.6–26.3	6.7	*Ceratophyllum* and Lily pads
J	0–24	20.4–31.2	6.4	*Ceratophyllum* and *Ludwigia*
K	0–24	20.8–24.0	6.4	*Ceratophyllum* and *Ludwigia*
L	0–30	20.4–29.0	6.2–6.5	*Ceratophyllum* and *Ludwigia*
M	0–24	19.0–21.0	6.4	*Potamogeton*
N	0–12	20.9–23.3	6.2–6.4	Water cress
O	0–24	17.0–22.5	6.4–6.5	*Potamogeton* and *Myriophyllum*
P	0–12	15.5–27.8	7.4	*Myriophyllum*

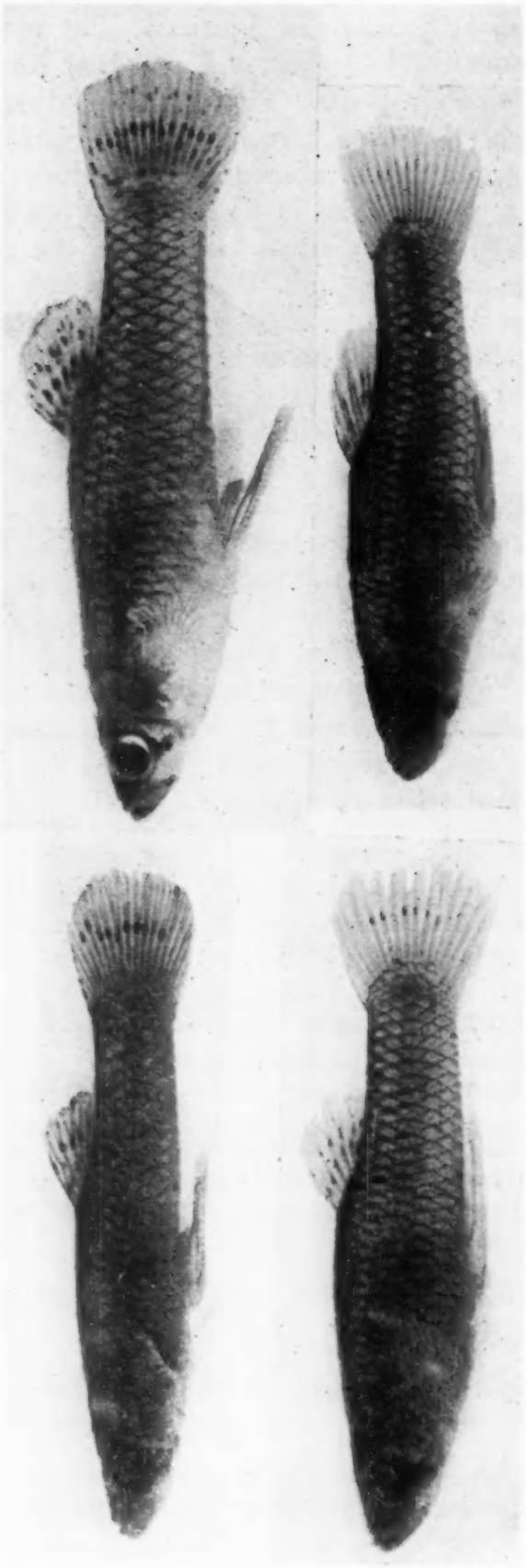

FIG. 4. Males from the Clear Creek hybrid swarm. Upper left: *G. affinis*. Lower left: wild-caught hybrid. Upper right: laboratory-reared hybrid. Lower right: *G. heterochir*.

ECOLOGY

General ecologic data for each station are listed in table 1. Temperature variations listed are not maximal. On the morning of November 30, 1957, when the air temperature was − 5° C., water temperature in the spring at station E was 20.6 while that at station F was 10° C. Spring boil temperatures vary between 20.5 and 21° C., thereby water temperatures near spring sources are relatively more constant than those far from the springs. No significant seasonal fluctuation of spring temperature was noted. Likewise, no seasonal variations in thermally plastic meristic characters is apparent. Minimum temperatures correlate better with other environmental factors than do maximum temperatures.

Total spring flow was relatively constant during the study period. There was a slight increase in water volume in 1957 after the heavy spring rains that year. However, during that summer, the spring at station L ceased flowing. Subsequently there was a slight increase in pH there. During the winter of 1956–57 the spring at station E moved from near some bathhouse steps 20 feet west to the base of a large willow. Water pH in the spring boils is relatively low and correlated with volume of flow; i.e., 6.1 to 6.2 in the large springs at stations K and O and 6.2 to 6.5 in the small springs at stations E, L, and N. Undoubtedly the pH values are partially due to relative concentration of CO_3^- and HCO_3^- ions as samples of spring water left standing for a month changed pH from 6.1 to 7.4; however, other factors must be involved as samples from stations K and P changed pH from 7.4 to 7.7 and 7.8 respectively during the same interval. It is likely that the aquifer comes through Permian rocks high in granitic (acidic) soils and flows to the surface through Cretaceous limestones (alkaline). Exposure to limestone would account for the rise in pH.

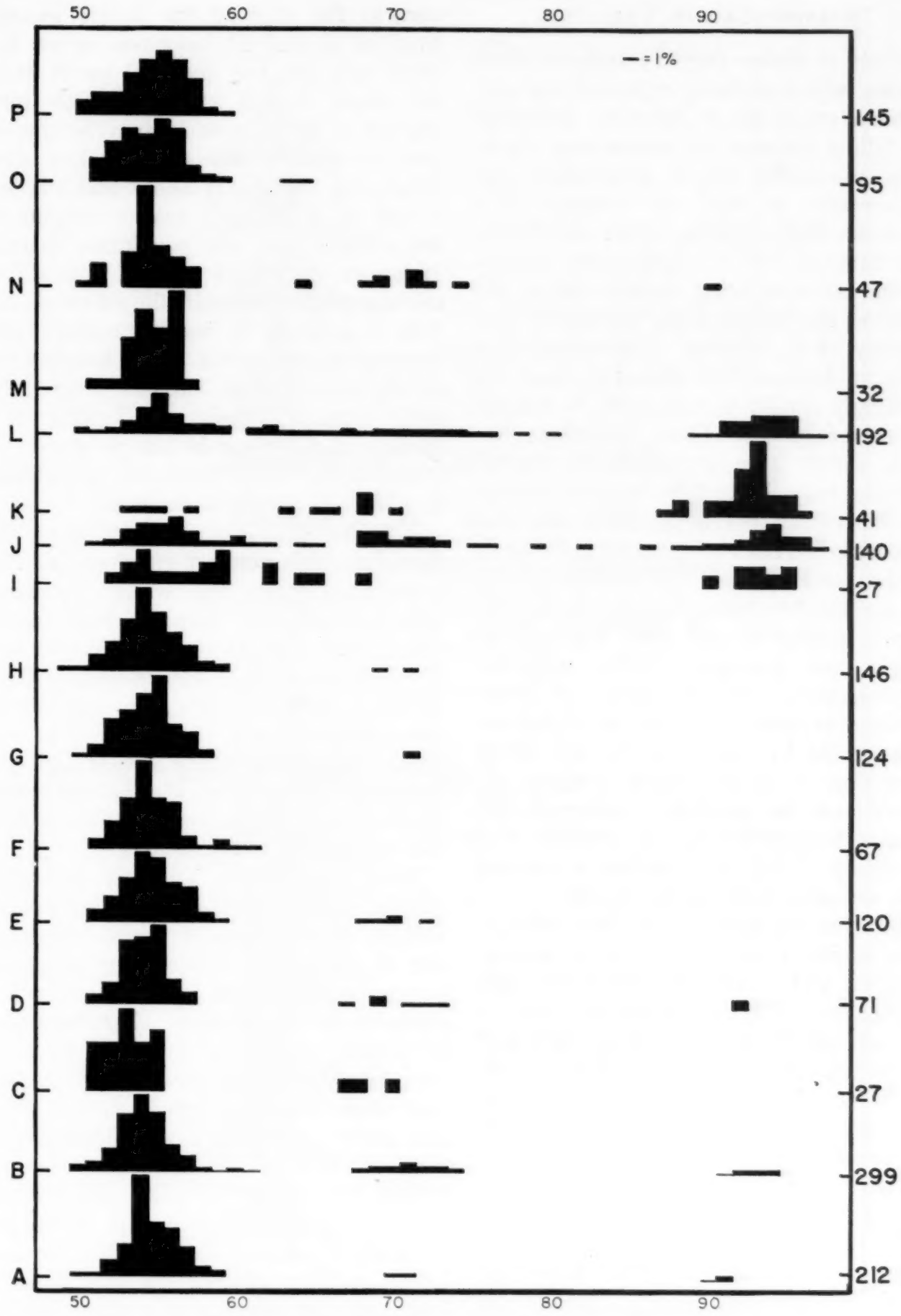

FIG. 5. Bar graph of coded phenotypic frequencies of male *Gambusia* populations of Clear Creek. The figures are rounded to the nearest per cent. A base line is given if less than one per cent of the population has this figure. The numbers of individuals used for the bar graph are given at right. Letters designating stations are given at left. All of the males with mature gonopodia were used, except two with obviously abnormal gonopodia.

Interpopulation Variation

Plots of males (fig. 5) indicate three modes, which probably represent the two parental stocks and F_1 hybrids. Individuals falling between the modes may represent subsequent hybrid generations and backcrosses as well as abberant F_1's (Suzuki, 1956; Hubbs, 1956; and Hubbs and Strawn, 1957). Laboratory experiments are now being carried out to determine the morphologic variability and fertility of F_1 hybrids. Laboratory F_1's have an intermediate phenotype and are strikingly similar to suspected F_1 natural hybrids (fig. 4). These laboratory hybrids differ from suspected F_1 natural hybrids only in having heavier bodies. As laboratory parental stocks are also deeper bodied than wild-caught individuals of the same species, this difference may be attributed to better diets in the laboratory. Similar results were obtained by Hubbs and Springer (1957) with related species. The frequency of intermediates between the modes for *G. heterochir* and the hybrids is significantly lower than that of intermediates between *G. affinis* and the hybrids. Although the relative frequencies may be artificial due to coding, I believe it indicates reduced back crossing with *G. heterochir*.

Samples of males from like habitats have similar plots. Those from stations I, J, K, and L all have relatively high frequencies of both species as well as hybrids, and have similar vegetation and water pH. Likewise, those from A, B, and D have few *G. heterochir* and hybrids but many *G. affinis*. The plant types and pH are similar.

There is a tendency for hybrid frequency in primarily *G. affinis* populations to be inversely correlated with distance from the hybrid swarm. The distance of hybrid migration is small. Hybrids are absent from P and only questionable intermediates occur at F. Both stations are 200 yards from the main hybrid swarm (stations I, J, K, and L). An abrupt change of hybrid frequency occurs at the edge of the hybrid swarm. Stations H and M have few or no hybrids and are less than 50 yards from the main hybrid swarm. (The total absence of hybrids at M may be due in part to sample size.) The low dam separating stations H and I and stations L and M respectively may contribute to the abruptness of the population change. However, as hybrids (and *G. heterochir*) are absent downstream, the effect of the dam is probably in making ecologic differences more distinct. The hybrids are closely restricted to habitats favored by both parental species. Likewise, frequency of *G. affinis* is low at station K which is the most distant from habitats in which *G. affinis* is dominant.

I believe that the distribution of the flora has a more direct effect on the fish populations than the water chemistry which is reflected in pH. Stations M and O have low pH (hybrid swarm) and *Myriophyllum* and *Potamogoton* flora (pure *G. affinis*). The fish populations are essentially pure *G. affinis*. The extensive adjacent offshore area of high pH has probably permitted *Myriophyllum* and *Potamogoton* to swamp the *Ceratophyllum* typical of low pH water.

Plots for females (fig. 6) follow a pattern similar to that of males except that no hybrid mode is noted. Perhaps this is due to this mode being obscured by the numerous *G. affinis* females because of the use of fewer characters and to growth changes of females. In general hybrid females are found less distant from the main hybrid swarm than are males. I feel that the difference is real. When a station is collected a second time within 24 hours, many more adult males are collected than immature or adult females. These males are believed to have entered the sample area because of the absence of resident males. Greater dispersal distance for males than for females has been demonstrated not only for many vertebrates (Blair, 1953 and ms; Fitch, 1940 and 1956; Fitch and Rainey, 1956; and Howard, 1949) but

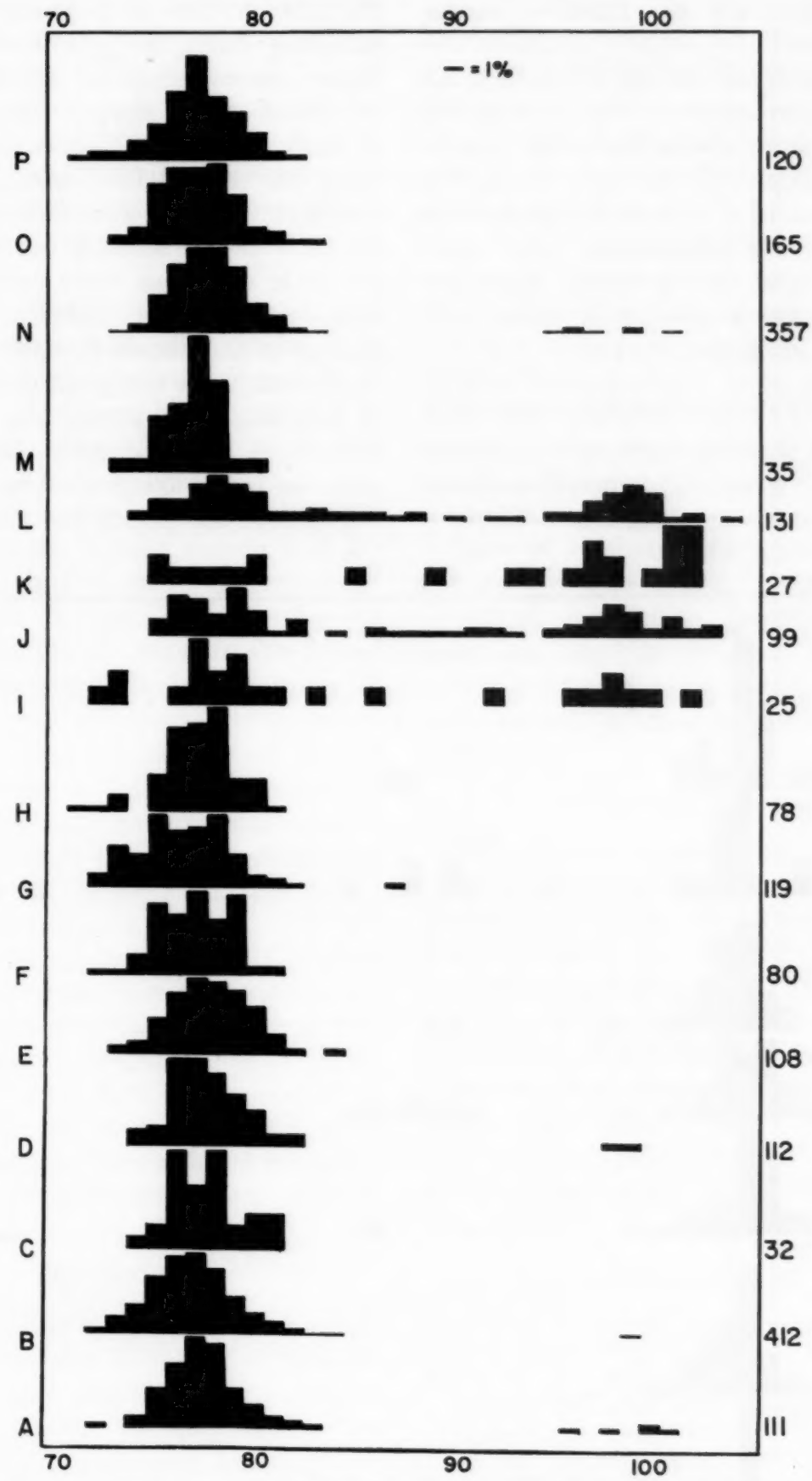

FIG. 6. Bar graph of coded phenotypic frequencies of female *Gambusia* populations of Clear Creek. The figures are rounded to the nearest per cent. A base line is given if less than one per cent of the population has this figure. The number of individuals used for the bar graph are given at right. Letters designating stations are given at left. All of the females 25 or more millimeters standard length were used, except for one without a dorsal fin and two with lateral chromatophores scraped off during collection operations.

also indicated for *G. affinis* (Hubbs, 1959).

Gambusia affinis modes for both sexes appear to approach to *G. heterochir* modes in samples from within the main swarm. Adjacent samples do not have this trend. Introgression of *G. heterochir* genes into these *G. affinis* populations may occur but if so, that introgression does not appear to have a phenotypic effect outside of the immediate swarm.

Temporal Intrapopulation Variation

The plots showing interpopulation variation (figs. 5 and 6) use all available material from each station. Thereby changes within a population between sampling dates are obscured. Most of these plotted temporal changes can be attributed to a sample size. That is: at stations G and H, both hybrid males were collected in 1957 and at station O, both hybrid males were collected in 1956. At each of the stations over one-half of the male *G. affinis* were collected at the same time as the hybrids. Temporal change in population structure at stations A, B, and N are too great to be attributed to sampling error alone. As the data for both sexes are essentially the same, only plots for males are given (fig. 7).

I believe the population change at sta-

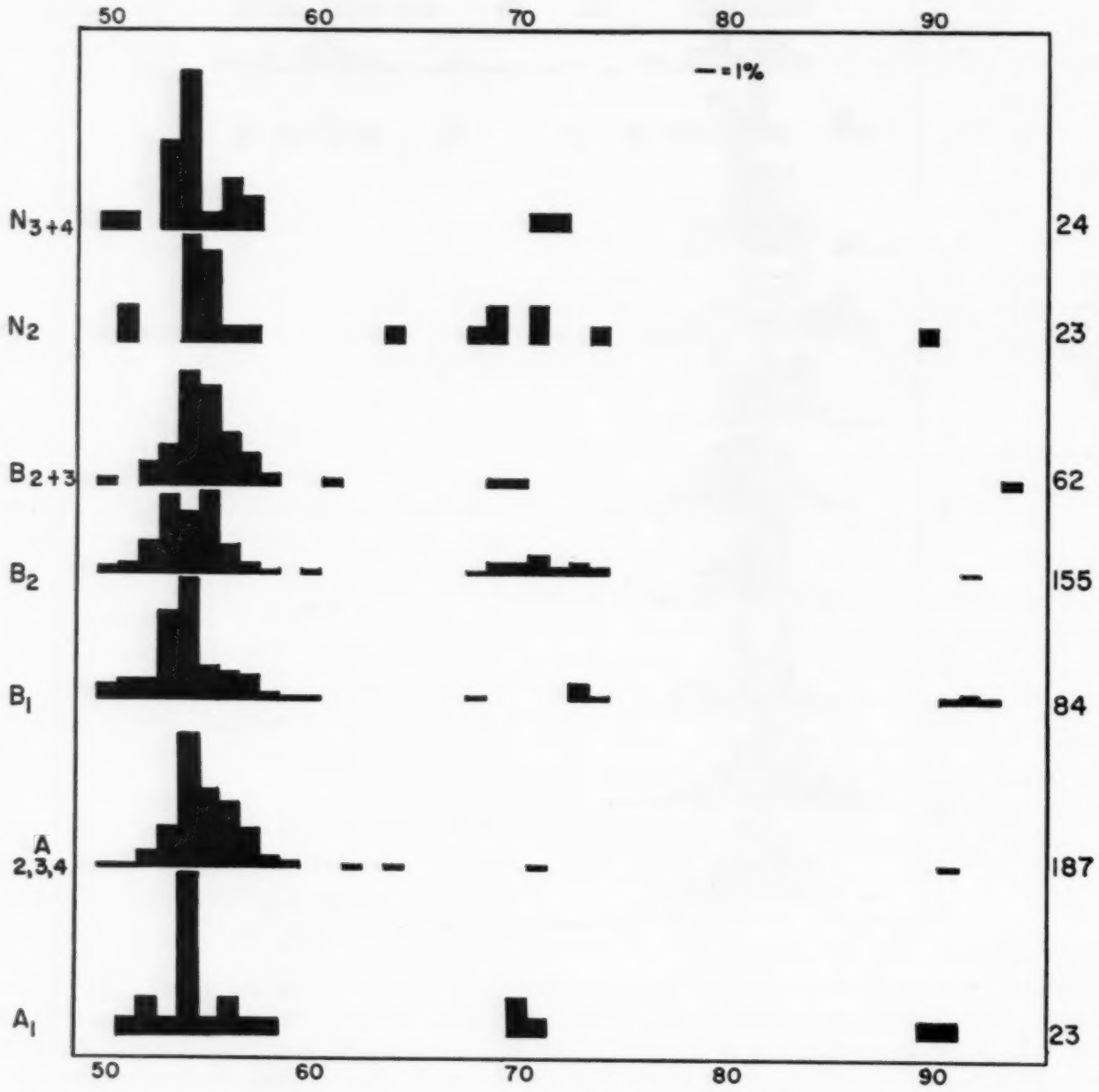

Fig. 7. Bar graph of coded phenotypic frequencies of male *Gambusia* population that changed during the study. The figures are rounded to the nearest per cent. The numbers of individuals used for the bar graph are given at right. Numbers at left designate the collection trip to the appropriate station.

tion N (no sample was taken during the first visit) is due to the effects of extensive collecting. The station is located in a small spring run adjacent to the impounded main stream. Heavy collecting in this limited habitat markedly reduced the population size and immigrants from station M would show little or no hybridization.

Population changes at stations A and B are correlated with changes in flora (table 1). The relative frequency of hybrids and *G. heterochir* is greatest in samples taken when plants were similar to those in the main hybrid swarm. Unfortunately the pH tests were first made in 1957 after the hybrid swarm and associated flora had essentially disappeared from stations A and B. Thereby no data are available to correlate the faunal and floral changes with changes in water chemistry.

Both inter- and intrapopulation studies show little effect of the hybrid swarm on the phenotype of the parental species either over a short distance or short time after one parent (always *G. heterochir*) was absent at a specific locality. Thereby there is a strong indication that *G. affinis* population pressure can successfully resist introgression of *G. heterochir* genes. As preliminary investigations indicate that *G. heterochir* does not reproduce in as cold water as does *G. affinis,* their hybrids might also have reduced fecundity in winter in thermally fluctuating environments.

Migration

Three possible alternatives are available to explain the frequency of hybrids and *G. heterochir* outside the main swarm area. One is that the populations are stable with little or no gene exchange. I feel this hypothesis to be untenable. It is difficult to visualize how hybrids would maintain themselves at stations with only one parental species (E, G, H, and O). Moreover, intermediates are relatively no more frequent away from the main swarm than at any station in the swarm.

It is possible that a population of *G. heterochir* occurs in the deep water of the old main channel of Clear Creek and that inshore hybrids come from this stock. The relative decrease in hybrid frequency with distance from the main swarm is not in accord with this hypothesis. Moreover, station C, immediately offshore of station B, shows no increase in hybrid or *G. heterochir* frequency. Likewise, extensive visual examination of offshore *Gambusia* populations from a boat and with self-contained underwater diving apparatus indicates that the populations below the upper dam were chiefly or entirely *G. affinis*.

Flow of *G. heterochir* genes probably follows the shore line. Not only are *Gambusia* population densities greatest here, but also the relative decrease in hybrid frequency with distance from the main swarm is in accord with this hypothesis.

Acknowledgments

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Literature Cited

Anderson, E. 1949. Introgressive hybridization. John Wiley and Sons.

Blair, W. F. 1953. Population dynamics of rodents and other small mammals. Adv. in Genetics, **5**: 1–41.

——. ms. Biology of the rusty lizard.

Fitch, H. S. 1940. A field study of the growth and behavior of the fence lizard. U. Cal. Publ. Zool., **44**: 151–172.

——. 1956. A field study of the growth and behavior of the Kansas ant-eating frog, *Gastrophryne olivacea.* U. Kan. Publ. Mus. Nat. Hist., **8**: 275–306.

——, and D. G. Rainey. 1956. Ecological observations on the woodrat, *Neotoma fori-*

dana. U. Kan. Publ. Mus. Nat. Hist., **8**: 499–533.

HOWARD, W. E. 1949. Dispersal, amount of inbreeding, and longevity in a local population of prairie deermice on the George Reserve, southern Michigan. Cont. Lab. Vert. Biol., Univ. Mich., **43**: 50 pp., 2 pls.

HUBBS, CARL L. 1955. Hybridization between fish species in nature. Syst. Zool., **4**: 1–20.

——, L. C. HUBBS, AND R. E. JOHNSON. 1943. Hybridization in nature between species of castostomid fishes. Cont. Lab. Vert. Biol., Univ. Mich., **22**: 76 pp., 7 pls.

——, AND K. F. LAGLER. 1947. Fishes of the Great Lakes region. Bull. Cranbrook Inst. Sci., **26**: xi + 186 pp., 26 pls.

HUBBS, CLARK. 1956. Relative variability of hybrids between the minnows, *Notropis lepidus* and *N. proserpinus*. Texas J. Sci., **8**: 463–469.

——. 1957a. *Gambusia heterochir*, a new poeciliid fish from Texas, with an account of its hybridization with *G. affinis*. Tulane Stud. Zool., **5**: 1–16.

——. 1957b. Distributional patterns of Texas freshwater fishes. Southwestern Nat., **2**: 89–104.

——. 1959. High incidence of vertebral deformities in two natural populations of fishes inhabiting warm springs. Ecology, **40**: 154–155.

——, AND V. G. SPRINGER. 1957. A revision of the *Gambusia nobilis* species group, with descriptions of three new species, and notes on their variation, ecology, and evolution. Texas J. Sci., **9**: 279–327.

——, AND K. STRAWN. 1957. Relative variability of hybrids between the darters, *Etheostoma spectabile* and *Percina caprodes*. EVOLUTION, **11**: 1–10.

SUZUKI, R. 1956. A study on the interfamiliar crossing between the minnow (*Gnathopogon elongatus elongatus*) and mud loach (*Misgurnus anguillicaudatus*). Bull. Aichi Gakugei Univ., **4**: 29–34.

CONTACT BETWEEN THE RANGES OF TWO ALLOPATRIC SPECIES OF POCKET GOPHERS

THOMAS E. KENNERLY, JR.

Department of Biology, Baylor University, Waco, Texas

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INTRODUCTION

This study was initiated to investigate the biological dynamics of two allopatric species of pocket gophers whose ranges are in contact. In southern Texas *Geomys bursarius attwateri* and *G. personatus fallax* reach distributional limits. Davis (1940) recorded a single specimen of *G. personatus* from Beeville, Bee County and Blair (1952) reported the occurrence of *G. bursarius* 11 miles east of Beeville. No significant environmental barriers were evident within this hiatus. Little is known concerning the factors responsible for the maintenance of allopatry in regard to species with similar ecological requirements particularly in a region devoid of significant ecological contrasts or breaks. These two species of pocket gophers in southern Texas present an excellent opportunity to study this enigmatic phenomenon.

METHODS

Field collecting proceeded irregularly between December 1952 and May 1955. Dead trapping was accomplished by means of pincher-type steel traps. Surface soil samples were taken at various trapping stations for color comparison with pocket gopher pelage. Color measurements were taken on both study skins and soil samples by means of a Photovolt Photoelectric Reflection Meter, Model 610. Red, green and blue color filters were used. Pelage color measurements were taken on the mid-dorsal line about two inches posterior to the shoulders on study skins. Only adult specimens in winter pelage were utilized. A white magnesium oxide block served as standard maximum with readings on pelage and soil samples expressed as percentage values. The Reflection Meter was readjusted if necessary after every ten readings. Coefficients of correlation of soil and pelage color measurements are presented in table 1.

DISTRIBUTION OF THE GENUS *Geomys*

This genus as a whole should be regarded as preferentially mesic. It has been recognized that the genus *Geomys* is highly partial to sandy, friable soils (Merriam, 1895; Davis, 1940) and that areas of indurate, non-friable soils, abundant woody vegetation, areas under intense cultivation and major water-ways act as usually effective barriers or deterrents to its distribution. As is the case with many species of vertebrates distributed along the Gulf coastal area of the United States, the species of *Geomys* exemplify an almost "classic" Post-pleistocene distribution, i.e., the climatic changes accompanying glaciation presumably resulted in a splitting of range into eastern and western groups which have not subsequently reunited. A western species complex occupies the Great Plains region involving much of the Mississippi-Missouri River valleys mainly west of the Mississippi River from Mexico to Can-

TABLE 1. *Coefficients of correlation of soil and pelage color measurements*

	No. of specimens	Reflected red	Reflected green	Reflected blue
G. personatus	25	.833	.833	.797
G. bursarius	23	.743	.608	.480

ada. An eastern species complex (4 nominal species) occurs widely in Florida exclusive of the southern third of the state and locally in southern Alabama and Georgia. Three species are included in the western *Geomys* complex: *bursarius, arenarius* and *personatus*. *G. bursarius* with 21 named forms from 16 states and Canada has by far the most extensive range of any species of the genus, occupying much of the Great Plains region from Canada south to the vicinity of the San Antonio River, Texas. *G. personatus* with seven named forms occupies much of the Texas Lower Rio Grande Valley north of the Rio Grande, replacing *bursarius* to the southwest from the vicinity of the San Antonio River. Locality records for these two species in the area of study are indicated in figure 1. Goldman (1915) described the subspecies *tropicalis* from Altamira, Tamaulipas, Mexico which is 250 miles from the nearest known population of *G. personatus*. This

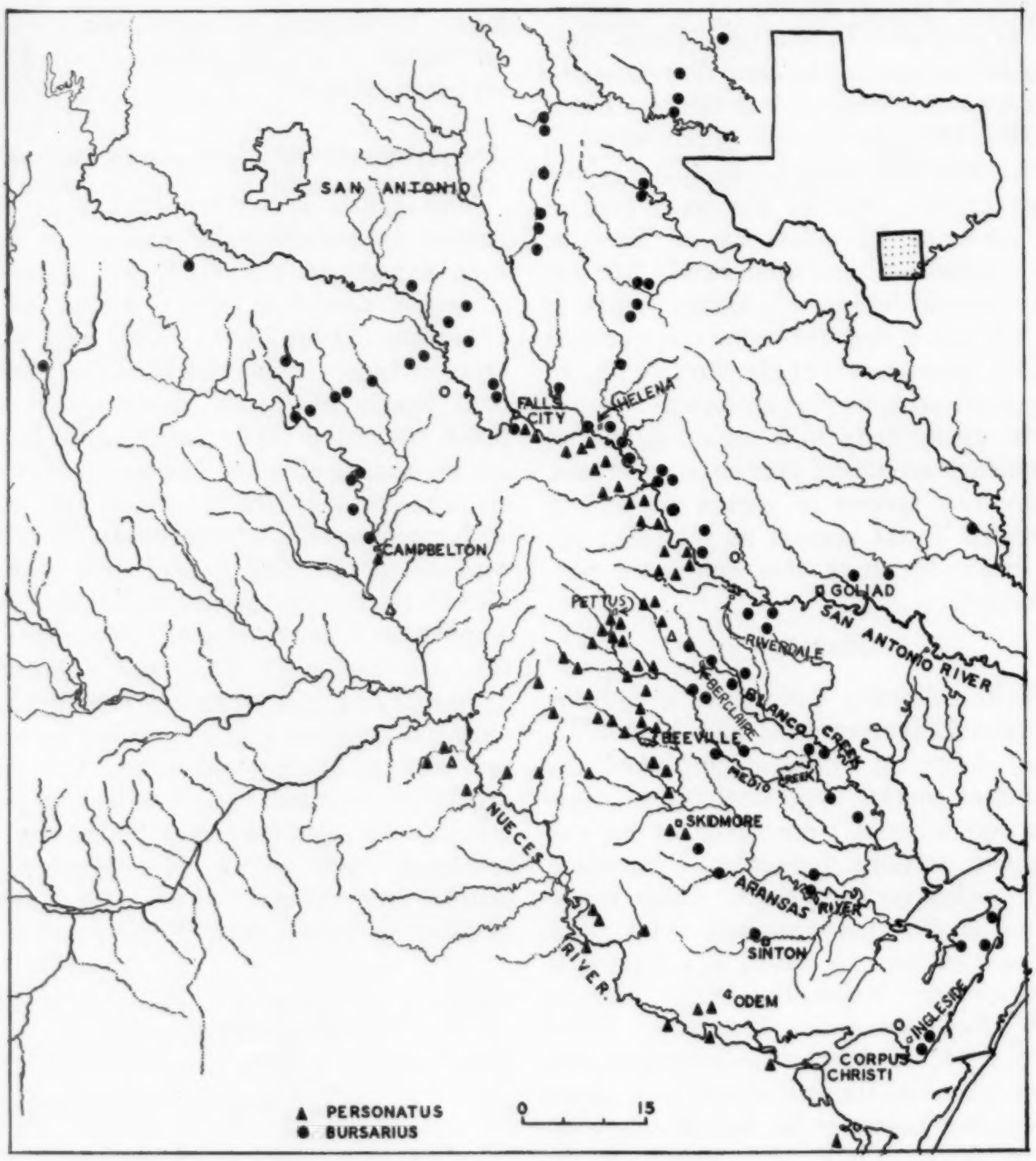

FIG. 1. Map of southern Texas depicting the peripheral ranges of *Geomys personatus* and *Geomys bursarius*. Hollow triangles and hollow circles represent sites where trapping was unsuccessful and presumably occupied by *G. personatus* and *G. bursarius* respectively.

apparently relict population has not been subsequently investigated. *G. arenarius* with two named forms occurs locally from the vicinity of El Paso, Texas through Luna, Dona Ana and Otero Counties, New Mexico along the Rio Grande and constitutes the westernmost extension of *Geomys*.

The Species *G. Personatus* and *G. Bursarius*-Morphological Diagnostics

G. personatus and *G. bursarius* are closely related species and qualitative diagnostic characters are apparently few. The most useful such character is the length of the dorso-lateral exposure of the jugal as compared with the width of the rostrum ventrad to the infraorbital foramina (Davis, 1940). In *personatus* the dorsal jugal exposure is longer than the width of the ventral rostrum and in *bursarius* it is shorter. The *personatus* pocket gopher is a distinctly larger animal than is *bursarius*. Essentially any skeletal measurement therefore should prove quantitatively diagnostic between the two species were a significantly large series involved of the same sex (sexual dimorphism is marked in the *Geomyidae*). Aside from a definite overall size difference, these two species differ in relative length of tail which is generally shorter both actually and proportionately in *bursarius* than in *personatus*. *G. personatus* is generally the darker of the two species in dorsal pelage color, tending toward blackish brown while *bursarius* tends toward russet brown. Ingles (1950) and Kennerly (1954) demonstrated a correlation between pocket gopher dorsal pelage color and substrate color of habitat. One might well expect widespread intraspecific populations of pocket gopher to show varying adaptive coloration in selective response to varying color of substrates although the direct physiological effect (if any) of moisture on pigmentation in mammals is virtually unknown. Parallelism in dorsal pelage color in different allopatric populations of pocket gophers is theoretically possible. In deference to these considerations dorsal pelage color was not attributed important diagnostic value. Ventral pelage color in the pocket gopher is seemingly "non-adaptive" and ventral color patterns are rather variable in both species. Despite the risk of over-simplification it would appear that, other factors being equal, less adaptive features in a population are more variable than more adaptive features which are subject to greater selective pressure. Or stated another way: an inverse relationship exists between the selective value of a feature and the variability of that feature in a population. In *bursarius* most or all of the venter is characteristically dark gray. If a white patch is present it is restricted to the pectoral region. In *personatus*, only the distal areas of the venter are dark gray, and an irregularly bordered white patch characteristically extends medially from the pectoral region to the inguinal region. A seemingly significant qualitative diagnostic is the curvature of the lambdoidal crest (Kennerly, 1958). Laboratory comparison of "contact" specimens of both species was undertaken carefully in order that any morphological reflection of hybridization or introgression might be noted. None was detected.

General Ecologic Position

Like other species of *Geomys, personatus* and *bursarius* are highly partial to sandy, friable soils. The genus seems generally mesic in moisture requirements and *bursarius* seems typical in this respect. The *bursarius* populations pertinent to this study occur primarily in a region which receives an average of 30 to 33 inches of precipitation annually (Norquest, 1941). Pertinent populations of *personatus* occur mainly in an area receiving an average of 26 to 30 inches of precipitation annually. Other populations of *personatus* occupy less mesic areas farther south and southwest to the Rio Grande River, the annual precipita-

tion here averaging between 19 and 26 inches. *G. personatus* therefore appears to be adapted to more xeric conditions than is *bursarius*. It has been suggested (Kennerly, 1954) that smaller size in the pocket gopher might have selective value in situations of indurate soils. *G. bursarius,* the smaller in body size of the two species, was taken in localities of relatively tight soils more frequently than was *personatus*. Thus *bursarius,* although typically partial to friable soils, seems to exhibit a greater tolerance for indurate soils than *personatus* does.

Ecological Relations

The following discussion is concerned with the ecological and topographical features of the region in which the ranges of these two species approach one another. The designation "approximation region" will hereafter refer to that portion of the Texas Coastal Plain between the San Antonio and Nueces River systems which extends generally north and south between the ranges of *personatus* and *bursarius*. Topographically the region is predominantly gently rolling hills except for the flat coastal belt. There is a low elevation-gradient from the vicinity of Falls City (307 feet) southward some 90 miles to the coast. Aside from a limited area along the coast, the region of approximation is a relatively well-drained region. The Atascosa River, a tributary of the Nueces River, and the upper San Antonio River and certain of its tributaries serve the northern approximation area, while the Blanco Creek, Medio Creek and Aransas River systems drain the southern portion. The presence of abundant tributaries and hence a network of numerous flood-plains has been a significant factor in the distribution and dispersal of the pocket gopher. The coastal area between Ingleside, San Patricio County, and the mouth of the Nueces River is poorly drained and virtually devoid of even minor tributaries.

The approximation area occurs in a region which is classified by Thornthwaite (1948) as dry subhumid, with a moisture-deficiency index of zero to − 20, and megathermal. No abrupt vegetative break coincides with the approximation area. It is rather a region of gradual transition (ecotone) from western thorny brushlands to eastern prairie grasslands and oak-hickory alternes. Characteristic xeric plant species of the thorny brushlands are: mesquite (*Prosopis juliflora*), several species of *Mimosa* and *Acacia,* granjeno (*Celtis pallida*), prickly pear (*Opuntia lindheimeri*), *Condalia* and tasajillo (*Opuntia leptocaulis*). Characteristic plant species of the Fayette and Coastal Prairies (Tharp, 1939) include: tall salt grass (*Spartina spartinae*), sage (*Savlia*), bluestem (*Andropogon*), *Stipa, Paspalum, Panicum,* dropseed (*Sporobolus*), grama (*Bouteloua*) and other grasses. From the vicinity of Rockport south, grasses show an increasing adaptation to deficient moisture as evidenced by a change in species and less often in genera (Tharp, *op. cit.*). Throughout the approximation area flood-plains commonly support well developed mesic woodlands of oaks (*Quercus*), elm (*Ulmus*), hackberries (*Celtis*), pecan (*Carya*) and other trees.

Faunal Distribution in Approximation Area

The approximation area is included within a region which has been noted as a region in which many vertebrates reach their distributional limits. Blair (1950) separated the Tamaulipan (west) and Texan (east) biotic provinces in this general area, actually demarked along the line separating pedocal and pedalfer soil types. The following mammalian species reach their northeastern limits in the Tamaulipan biotic province (although some extend north and northwest beyond the limits of this biotic province) and have no intrageneric counterparts east of the vicinity of the boundary with the Texan biotic province: *Aello megalophylla, Conepatus leuconotus texensis, Dipodomys ordi sennetti, Felis*

yagouroundi cacomitli, Liomys irroratus texensis and *Notiosorex c. crawfordi. Blarina brevicauda* occurs only in the eastern approximation area. Of greater significance to the problem at hand are other mammals which manifest a specific or subspecific "break" from east to west within the general region of approximation and have representatives on both sides of this area. Forms displaying this interruptive distribution phenomenon are: *Baiomys t. taylori* and *B. taylori subater, Cryptotis parva berlandieri* and *C. p. parva, Didelphis marsupialis texensis* and *D. marsupialis pigra, Oryzomys couesi aquaticus* and *O. palustris texensis, Reithrodontomys fulvescens intermedius* and *R. fulvescens aurantius, Scalopus aquaticus alleni* and *S. aquaticus cryptus* and *Spilogale gracilis leucoparis* and *S. putorius indianola,* listed from west to east respectfully. *Cryptotis p. parva* has been recorded in east Texas (Davis, 1941) but the extent of the hiatus between this race and *C. parva berlandieri* is poorly known. It should be pointed out that several mammals range across the approximation area from east to west without interruption so far as is known. Two examples are: *Peromyscus leucopus texanus,* occurring west to the mouth of the Pecos River, east to Galveston Bay and *Perognathus m. merriami,* south to Tamaulipas, Mexico and east to western Louisiana. In addition there are many reptiles and amphibians which reach distributional limits or show a specific or subspecific break in this region. A few of these forms are: *Anolis carolinensis, Hyla cinerea, Masticophis taeniatus schotti, Sceloporus variabilis* and *Tantilla nigriceps.* Thus in terms of vertebrate distribution it is clear that this region of approximation is a critical one, interrupting those having different representatives on each of this zone and limiting other forms which occur on but one side of this zone. At the risk of over-simplifying the problem, this area seems to be a region of intermediate ecology, particularly moisture, supporting a biota which consists of an admixture of mesic (eastern) and xeric (southwestern forms).

Pocket Gopher Distribution in Approximation Area

Patterns of distribution affect frequency of migration between populations and thereby influence divergence of local populations. The family *Geomyidae* is notoriously wealthy in trinomial designations. Restricted locomotor capacities and the existence of numerous, small isolated or semi-isolated populations have promoted local differentiation to a degree seldom displayed in mammalian groups. Figure 1 depicts the known distribution of *G. personatus* and *G. bursarius* in the region of approximation. Pocket gophers of this genus have been considered in the past to display "island model" (Wright, 1943) patterns of distribution, i.e., occurring locally within delimited areas of favorable soils (Davis, 1940; Kennerly, 1954). This is unquestionably true in regions of generally sandy soils variously interrupted by physical and ecological barriers where the pocket gopher occurs extensively. Here the distribution pattern is "areal" when considered regionally, although many populations may not be geographically continuous. Within most of the region considered in this study, however, the occurrence of both species of pocket gopher showed a distinct correlation with alluvial terraces and adjacent areas of friable soils accessible to alluvial situations and consequently should be regarded as basically "dendritic" (Thornton and Al-uthman, 1952) in distribution pattern. This distribution pattern suggests that ancestral stocks of both species populations involved in this study were coastal in position and that emigration proceeded inland utilizing alluvial soils as avenues for dispersal. It seems that throughout the range of both species such flood-plain routes have significantly facilitated dispersal.

The ranges of *personatus* and *bursarius* were observed to approach one another at seven localities and actually contact at

one locality. In none of these cases does a river barrier exist between the ranges of the two species but at one locality there does appear an evident barrier of indurate soil. It is almost axiomatic that the geographic range of a given animal is dynamic. This is certainly the case with the pocket gopher. Population density and hence distributional range is undoubtedly affected by such environmental factors as periodic inundation in the proximity of river systems and prolonged periods of drought.

Localities of Approximation

Campbellton: Near the town of Campbellton, Atascosa County, the ranges of the two species approach one another. The author collected *personatus* one and one-half miles south of Campbellton and *bursarius* six miles north of Campbellton. The hiatus in this case is seven and one-half miles or less. However, Davis (1940) reported *bursarius* two miles north of Campbellton which would reduce the hiatus to three and one-half miles. In March 1954, this above-mentioned site was investigated by the author and found to be devoid of pocket gopher workings, evidencing the dynamic nature of pocket gopher distribution. The area of hiatus between ranges in the vicinity of Campbellton is a region of alluvial deposits along the Atascosa River and appears favorable for pocket gopher habitation. Thus the Campbellton hiatus is free of evident barriers to pocket gopher dispersal.

Riverdale: Riverdale, Goliad County, is located on the west bank of the San Antonio River. The great significance of this locality in relation to the distribution of both species will be discussed subsequently. In this area the hiatus between the two species is approximately eight miles; *personatus* was collected five miles west of Riverdale and *bursarius* was collected three miles south of Riverdale on the west side of the San Antonio River. Both species were taken on sandy soils. The gap between ranges in this locality is a region of dark heavy soils which is under intensive cultivation. No pocket gopher workings were observed within this hiatus and it is thought that this area of tight soils constitutes a formidable barrier to dispersal. At this locality the banks of the San Antonio River are precipitous and alluvial deposits seem confined to the immediate vicinity of the river.

Pettus-Berclaire: This locality is so designated because an approach of the ranges of the two species was discovered along Highway 883 between the towns of Pettus, Bee County, and Berclaire, Goliad County. The species *personatus* was collected nine and one-half miles northwest of Berclaire and *bursarius* was collected five miles northwest of Berclaire. This represents an apparent hiatus of four and one-half miles. However, pocket gopher workings were observed at a site almost precisely midway between the two above-mentioned localities. This burrow was repeatedly trapped without success. There are several factors which point to *personatus* as constructor of this burrow. First, there is continuous sandy soil between the site of *personatus* capture and the site where trapping was unsuccessful, a distance of approximately three miles, although south of the latter site the soil becomes rocky and indurate. Clayey soils occur in the gap between the *bursarius* collecting site and unknown workings. The specimen from the *bursarius* site was collected at the apparent fringe of a friable soil area which extends northwest from the vicinity of Berclaire. It appears therefore that a relatively narrow barrier of tight soils separates the *bursarius* site from the sites of of the presumed *personatus* burrow and known *personatus*. Richland Creek is a north-south intermittent water-way west of the vicinity of these sites but the associated alluvial deposits seem inadequate for pocket gopher dispersal. Another factor which suggests that the unknown burrow belongs to *personatus* is the character of the burrow and mounds. In addition to characteristically large mounds like those of *personatus*, the diameter (81 mm.) and depth (265 mm.) of the unknown burrow compare favorably with typical *personatus* burrow dimensions (Kennerly, 1958). Whichever species occurs at this site, the hiatus between ranges is at least two miles.

Normanna-Medio Creek: In this area, collecting sites for both species were located on opposite sides of Medio Creek but about seven miles apart. Three miles southeast of Normanna, Bee County (one mile south of the southwest bank of Medio Creek), *personatus* was recorded. Pocket gopher workings, typical of *personatus*, were also noted on the immediate southwest bank of Medio Creek. A specimen of *bursarius* was collected on the northeast bank of Medio Creek at the point of intersection of Medio Creek and Highway 59. The hiatus between ranges is about seven miles. However, this gap is very probably less since alluvial terraces along this water-way, particularly along the northeast bank, seem adequate for pocket gopher dispersal. There are adjacent sandy regions, again to the northeast, in the vicinity of the *personatus* collection site southeast of Normanna. It seems probable that in this area Medio Creek is the southwest boundary for *bursarius* as this species was not found to occur on both sides of Medio Creek

southeast of Normanna. However *bursarius* occurs on both sides of Medio Creek farther south. Indurate soils virtually border the southwest bank of Medio Creek. This may explain why *bursarius* has apparently failed to push northward along the southwest bank of Medio Creek opposite its present position on the northeast bank. Thus edaphic factors appear to encourage contact between these species along the northeast bank of Medio Creek.

Beeville-Medio Creek: The region from Beeville, Bee County, east to Medio Creek is an area of semi-friable soils. The species *personatus* occurs in the town of Beeville, but was not recorded east of there. The species *bursarius* was collected on the southwest bank of Medio Creek at the intersection with Highway 202, approximately eight miles eastsoutheast of Beeville. The evident hiatus between ranges in this locality is no more than eight miles, but the gap is undoubtedly less. Pocket gopher workings were noted approximately five miles east of Beeville and a burrow there was trapped unsuccessfully. Tentative identification of burrow and mounds with one or the other species of pocket gopher is rendered less reliable in areas of semi-friable soils since under such conditions specific characteristics are not distinctive. Such conditions obtained at this site. The hiatus for this region therefore is probably not more than five miles. Another specimen of *bursarius* was recorded approximately two miles east of Medio Creek, again in an area of semi-friable soils. It is possible that this region excludes the larger *personatus* but not the smaller *bursarius* as smaller size in fossorial forms may increase tolerability to less friable soils. This area is the farthest north locality where *bursarius* was collected southwest of Medio Creek. Southward to the coast, a distance of about 45 miles, *bursarius* ranges extensively south of Medio Creek. Therefore, within a distance of eight or nine miles northwest of the Beeville-Medio Creek locality, *bursarius* evidently reaches its distributional limits along the southwest bank of this water-way.

Skidmore: Edaphic factors appear to play an important role in this locality. The region between Beeville and Skidmore, Bee County, is comprised of dark but relatively sandy soils and *personatus* was common here. Immediately south of Skidmore, however, the soils become black and noticeably less sandy. The species *personatus* was collected within this area of semi-friable soils one mile south of Skidmore and *bursarius* was collected three miles south of Skidmore within the same region of adverse soils. The hiatus between ranges is no more than two miles. *G. bursarius* is known to range southeast of this site but its range north and northeast to Medio Creek is unknown. This locality was investigated periodically over a period of 18 months and pocket gopher workings were never observed within this two mile gap. No edaphic changes were noted within the actual hiatus and no water-ways exist here. It therefore appears that *personatus* has effected a minor inroad into the semi-friable soil area south of Skidmore and that no apparent physical or ecological barrier maintains this hiatus. Specifically, there is no evident barrier to the northward dispersal of *bursarius* save the presence of *personatus,* a possibility which will be discussed subsequently.

Sinton-Odem: The ranges of *personatus* and *bursarius* are known to approach within approximately nine miles of one another in the Sinton-Odem area, San Patricio County. A. G. Flury, Texas Game and Fish Commission, has kindly provided a specimen of *bursarius* collected along the alluvial terrace of Chiltipin Creek at Sinton, Texas. Two *personatus* collecting sites are pertinent to this area: two and one-half miles southwest of Odem and one mile east of the junction of Highways 9 and 894 (approximately six miles southeast of Mathis). This region of sandy soils between the known ranges of the two species seems to be adequate for pocket gopher habitation. However, most of this region has been denuded of natural vegetation and is currently under intensive cultivation. Extensive plowing not only destroys burrow systems but also obliterates for relatively long periods of time herbaceous roots and tubers which are necessary sustenance for pocket gophers (Aldous, 1951). If cultivation is responsible for the exclusion of pocket gophers in this region, the hiatus between the ranges is probably much wider today than formerly.

Coastal hiatus: The hiatus between the ranges of *personatus* and *bursarius* is greatest in extent along the coast, about 18 miles, between the mouth of the Nueces River on the west and approximately two miles west of Ingleside, San Patricio County, on the east. This region which is seemingly devoid of pocket gophers extends northward from the coast no farther than Sinton. The soils of this coastal belt are black loams developed on the Pleistocene Beaumont Clay. These are indurate soils. This region constitutes a doubly formidable barrier to pocket gopher distribution because almost the entire region is under intense cultivation. Approximately two miles nortwest of Ingleside, the Beau-

mont clays are abruptly replaced by quartzose dune sands along an east-west line. This abrupt soil change is dramatically emphasized by the occurrence of *bursarius* at the immediate northern border of dune sands and ranging throughout the dune sand area to the northern termination of Aransas Bay. The significant factor in consideration of the barrier effect of the Beaumont clays is that a "belt" of dune sands does not fringe the coast between Ingleside and the mouth of the Nueces River. Consequently, even along the immediate coastline there seems to be no avenue for pocket gopher dispersal. It should be pointed out that both species do occur on portions of the Beaumont Clay. The reasons for the occurrence of each species on this formation seem to be different. The species *personatus* occurs in the vicinity of Edroy and Odem, as previously mentioned, but in this region the Beaumont Clay is heavily impregnated with sand and within the tolerances of this species. Farther to the east *bursarius* occurs sporadically in San Patricio, Refugio and Bee Counties at Sinton, Papalote, Woodsboro, Balconia and Refugio. The Beaumont formation in this area consists mostly of clays with little sand. It is evident that *bursarius* has taken advantage of alluvial channels for dispersal into relatively adverse edaphic situations, utilizing such water systems as Chiltipin Creek, Blanco Creek, Medio Creek and the Aransas River. The *bursarius* pocket gophers are generally confined to these alluvial terraces, but in some localities *bursarius* has invaded adjacent situations of semi-friable soils, e.g., southeast of Skidmore. So far as is known, *personatus* does not occur within these semi-friable black soils except for the slight inroad southeast of Skidmore. With the possible exception of the Aransas River, there are no alluvial channels which would afford *personatus* entry to these adverse soils as drainage of this region is chiefly to the east rather than the west. However, further investigation might reveal that *personatus* follows the alluvial terraces of the Aransas River southeast into the Beaumont Clay from the vicinity of Skidmore.

Falls City contact: This locality represents the northernmost record for *personatus* (except *G. p. fuscus* at Del Rio, Texas), a range extension of about 35 miles over that recorded by Blair (1952). Approximately one-half mile south of Falls City, Karnes County, on the alluvial terrace of the south bank of the San Antonio River, specimens of *bursarius* and *personatus* were taken on opposite shoulders of the Arnold School highway. This paved highway runs north and south and the specimens of *bursarius* and *personatus* were trapped on the west and east shoulders of the highway respectively. Distributional data indicate that at this site *personatus* dispersal pressure should emanate from the southeast and *bursarius* dispersal pressure from the west. Therefore in theory the two species would be orientated "properly" from west to east. However, the orientation of species at this locus is considered fortuitous. This narrow paved highway would not constitute a barrier to pocket gopher dispersal for in other areas burrows seem to underlie paved roads from one shoulder to the other and in addition, pocket gophers could easily cross such highways on top of the ground. It is highly probable that this contact between species occurred before the advent of this highway. This was the only instance in which the two species were collected at the same site. Technically this constitutes "overlap" of ranges as the specimens were captured within about 18 feet of one another and presumably this distance is considerably less than the dispersal distances of both species. However as occurrence of these two species at the same site was unique in this study and as "overlap" of ranges is ordinarily thought of in terms of several miles, the ranges of these two species are considered as coming in contact without "overlap," i.e., parapatric. This relationship between species populations seems devoid of popu-

lation interaction, thus the term "parapatric" is deemed more appropriate than "coexistence." Both contact-captures were females, the *personatus* specimen was fully adult and the *bursarius* specimen slightly sub-adult. Both specimens were entirely characteristic of their respective species and no evidence of hybridization or introgression was apparent. As previously mentioned, the most diagnostic morphological character of these two species is the length of the jugal relative to the ventral width of the rostrum. In *personatus* the jugal is longer and in *bursarius* it is shorter. On specimens from the Falls City contact, these measurements were as follows: *personatus,* jugal—6.1 mm., ventral rostral width —5.0 mm.; *bursarius,* jugal—3.2 mm., ventral rostral width—4.9 mm. The diameter of the burrow of the *bursarius* female specimen was 76 mm. and that of the *personatus* female was 96 mm. comparing favorably with burrow diameter averages of about 70 mm. for *bursarius* and about 81 mm. for *personatus.* Thus, at the Falls City site, *bursarius* and *personatus* give evidence of being good species by parapatry without indication of interbreeding.

Role of the San Antonio River: The San Antonio River is a significant and somewhat enigmatic factor affecting the distribution of these two species of pocket gophers. For a distance of about 55 miles this river acts as the precise boundary between the ranges of *bursarius* and *personatus.* At five different stations (encompassing both banks of the river) between Helena, Karnes County, on the north and Charco, Goliad County, on the south, approximately 35 miles apart, specimens of *personatus* and *bursarius* were collected in the immediate vicinity of opposing west and east banks respectively. Separation of the two species by this river seems complete between Hobson, Karnes County, and the vicinity of Riverdale, Goliad County. Nowhere along this front was either species observed to have crossed the river. Permanent water-ways of significant flow have been considered effective barriers to pocket gopher movement (Davis, 1940) although only the Mississippi River has effectively prohibited eastward dispersal of members of this genus along the Gulf Coast. The San Antonio River is not a major water-way, averaging between 25 and 40 feet wide throughout the "boundary" region between the two species. The Nueces River which exceeds the San Antonio River in annual flow has not constituted an effective barrier to the dispersal of *personatus* as this species occurs extensively on both sides of the Nueces River. In addition, *bursarius* occurs extensively on both sides of the San Antonio River north of the vicinity of Falls City and south of the vicinity of Riverdale. Therefore the San Antonio River cannot be regarded an effective barrier to pocket gopher dispersal, but only as a "boundary" between the ranges of the two species along a considerable front. In view of this fact it seems highly significant that, with the exception of Falls City, *bursarius* and *personatus,* although separated by only the width of the river, have not crossed this "boundary" as far as is known and are not known to display parapatry on the same side of the San Antonio River.

Ecological Preferences

There are indications that *personatus* and *bursarius* have intrinsic differential ecological preferences. Applicable ecological factors would seem to include such evident variables as vegetation, climatic conditions such as moisture and temperature and edaphic factors.

Vegetation: As there is no abrupt vegetative change coincident with the line of approximation between the ranges of *personatus* and *bursarius,* any differences with regard to vegetation preference seems to resolve to the question of selective sustenance. Pocket gophers are strictly herbivorous but virtually nothing is known of the actual diet of any species. The universal technique of stomach anal-

ysis may not be applied to the pocket gopher because rapid digestive action renders stomach samples almost wholly unidentifiable. Aldous (1951) found that *Thomomys talpoides moorei* in Utah consistently cut away the vegetation from around a tunnel opening before constructing a mound. Most of these cuttings are apparently transported to store-rooms within the burrow system and he recorded a total of 48 plant species from caches in store-rooms and cuttings above ground. The pocket gophers considered in this study probably manifest a similar habit as the ground beneath mounds of *personatus* and *bursarius* was noted to be cleared of vegetation. However mound construction seems to be fortuitous and unorientated and it does not seem probable that all plant species encountered in the proximity of a proposed mound would be included as sustenance. Further, it has not been demonstrated that all plant species stored within the burrow system constitute food staples. In the approximation area *personatus* and *bursarius* occur in localities supporting a similar or identical flora. Thus any differential in diet implies a preferential selection of food items. Such action would tend to lessen interspecific competition for food and thereby would contribute little to maintenance of the striking allopatry displayed. It might be assumed *a priori* that two closely related species of pocket gophers occurring in the same region would display similar food habits in response to similar available foods. In deference to these considerations, food habits of *personatus* and *bursarius* in the approximation area are thought to be quite similar.

Climate: Temperature effects on pocket gopher distribution are not clearly understood. Subterranean existence is accompanied by significant reduction of temperature variations and results in relatively stabilized thermal conditions. Vorhies (1945) reported that, even at the hottest periods, the temperature of the air inside desert heteromyid burrows never exceeds 33° C. The constancy of such a microclimate applies even more strongly to pocket gophers as their burrows are almost always closed to the ground surface. Tolerances to temperature extremes have not been determined in the pocket gopher. *Geomys personatus* undergoes at least two molts annually, which result in short, sparse, light colored pelage during summer and long, thick, darker pelage during winter. *G. bursarius* was noted to develop typical summer pelage during the spring months of 1954 and 1955. Thus both species seem equipped, at least superficially, for relatively wide temperature tolerances. It is probable that the selective advantage of seasonal molts in ancestral geomyids lessened with the acquisition of fossorial existence. *G. personatus* may prove to have a higher temperature tolerance than *bursarius*, as the former species occupies a generally warmer region. The existence of a relict population of *personatus* in Tamaulipas, Mexico, further suggests megathermal adaptation. Thus, differences in temperature tolerances (preferences) between *personatus* and *bursarius* seem insignificant as applied to respective distributions in the region of approximation, particularly in view of the relatively constant microclimate of fossorial existence.

Moisture relations of the two species deserve attention. The species *bursarius* is distributed almost wholly within the area of "moisture-surplus" (Thornthwaite, 1948) and *personatus* is distributed entirely within an area of "moisture-deficiency." It is reasonable to assume that *bursarius* is generally adapted to more mesic conditions than is *personatus*. The precise manner in which moisture conditions limit the distribution of pocket gophers is not clear. No member of the family *Geomyidae* is known to take free water under field conditions. All are adapted to xeric environments to this extent. The gradient of moisture-decrease southward along the Texas coast is by no means constant and this situation applies as well to the region at least 75 miles inland. Average annual precipitation

drops from 38 inches at the longitude of northern Matagorda Island southward to 30 inches near Aransas Pass, which is near the approximation line between the ranges of *bursarius* and *personatus*. Thus within a distance of 55 miles the average annual precipitation drops eight inches. From Aransas Pass south to the Lower Rio Grande Valley, a distance of about 140 miles, the precipitation drops only six inches. It is evident that *bursarius* experiences a rapid decrease in available moisture as it approaches the southern periphery of its range. Yet increasingly xeric conditions (conversely for *personatus*) do not explain the abrupt approximation line phenomenon which the ranges of these species display. Another factor which merits consideration is the effect of moisture on the friability of soils. This will be subsequently discussed.

Edaphic factors: Although the genus *Geomys* is partial to sandy, friable soils, differences appear to exist between *personatus* and *bursarius* with regard to tolerance of less friable soils. Correlation of pocket gopher records with soil type reveals an apparent difference in specific tolerance to adverse soils. Of 101 *personatus* records, 32 or 31.7% were from sites of dark, loamy soils while 69 or 68.3% were from sites of light colored sandy soils. Of 51 records of *bursarius,* 23 or 45.1% were from loam sites and 28 or 54.9% were from sandy sites. Thus, *bursarius* exhibits a seemingly greater tolerance to soils with a high clay content than does *personatus* and perhaps this is because smaller size in fossorial forms may be advantageous in situations of less friable soils. Size alone is probably not the total explanation since the large *Cratogeomys* of western Texas, New Mexico and Mexico is known to occur commonly in areas of indurate, rocky soils. Moisture content probably affects friability of clay soils, a higher moisture content increasing friability. In *Geomys,* in which sandy soils are preferred, this factor would theoretically afford a pocket gopher of mesic environment greater available areas for habitation than a pocket gopher of xeric environment. If this is true, *personatus,* inhabiting largely a semi-arid environment, would occur chiefly on areas of sand, i.e., soils consisting of large particles, as it does. It is clear that not one but several factors influence specific toleration of soil types. However, specific differences in soil tolerance do not explain the abrupt contact line phenomenon as both sandy and indurate soils are distributed irregularly throughout the ranges of both *personatus* and *bursarius* in the region of approximation.

Barriers to Distribution

Rivers: River systems which are permanent and of significant flow act as barriers to the movement of pocket gophers (Davis, 1940). The most prominent water-way in the approximation region is the San Antonio River but this river is apparently not a formidable barrier since in certain areas *bursarius* occurs on both sides. There are several water-ways throughout the contact region which limit pocket gopher movement but do not constitute effective barriers to dispersal. These water-ways, persistent throughout most of their length, include the Aransas River, Blanco Creek and Medio Creek.

Vegetation: Dense stands of woody vegetation with accompanying complex root systems impede movement of pocket gophers. This phenomenon was noted with regard to *personatus* distribution in Live Oak County, but this type of barrier was not observed to be important in any of the approximation localities. Regions devoid of vegetation such as extensively plowed cultivation areas or bare stretches of coastal sand seem to offer more serious impediment to dispersal. This (plowed region) is apparently the situation in the sandy region between Mathis and Sinton.

Soil: In the approximation region, areas of indurate soil seem to be the

most effective evident barriers to distribution. In the following localities, areas of tight soils are thought to constitute the critical and perhaps sole barrier separating the ranges of *personatus* and *bursarius*: Riverdale, Pettus-Berclaire, Skidmore (?) and the coastal hiatus.

Interspecific competition: There is evidence that interspecific competition between *bursarius* and *personatus* plays a role in the maintenance of allopatry. Approximation between the ranges of other North American species of mammals seems to occur coincident with distinct and abrupt ecological changes so that the species involved are in reality at the periphery of their respective habitats. In the case under study, however, no abrupt change in environment coincides with the approximation of ranges. The environment is rather a transition region wherein the most impressive ecological change is the relatively rapid decrease of available moisture from east to west. Even under these conditions the meeting of a xeric species and a mesic species would normally involve at least occasional overlap of ranges or interdigitation, perhaps in significant proportions. Yet overlap of the ranges of *personatus* and *bursarius* was never observed, and these species are known to display parapatry at only one locality (Falls City).

The breeding seasons (at least the important winter peak) occur synchronously in *personatus* and *bursarius* and their ranges are known to approach one another closely at several localities apparently free of intervening barriers. The opportunity for gene exchange seems to be present. Specimens from contact localities were carefully analyzed but no evidence of hybridization or introgression was noted. Interspecific competition may clarify the enigmatic distribution of these species along a considerable extent of the San Antonio River. Along a boundary of over 50 miles *personatus* is confined to the west bank and *bursarius* is confined to the east bank. As *bursarius* occurs on each side of this river both to the north and south of the "boundary" region, this river is obviously not an effective barrier to dispersal. There are no apparent ecological differences between pertinent east and west sides of the river. There seem to be two possible explanations for this enigmatic distribution. First, it is possible that both species have become distributed along opposite banks of this river rather recently and that insufficient time has transpired for either population to effect a crossing. On the other hand, one or both species may have effected crossings in the past but have been unable to consolidate establishment of the "beach-head" due to unknown ecological factors or more probably interspecific competition. In deference to evidence that *personatus* is expanding its range at the expense of *bursarius,* the former explanation is favored. It seems significant that in areas where *bursarius* occurs on the west side of the San Antonio River, north of Falls City and south of Riverdale to the coast, *personatus* is absent from the vicinity of the river and occurs 20 to 50 miles to the west. The possible explanations for the absence of *personatus* here will be discussed later.

The precise manner in which two fossorial species might compete is not clear. Aside from a situation in which two species with identical nutrient requirements might deplete an acutely limited food supply, competition for food is difficult to imagine because comparative efficiency at food procurement would not appear to be competitive. Individuals of both species would derive sustenance independently from their respective burrow systems (pocket gophers are solitary, exclusive of the breeding season). It seems more feasible to consider the possibility of physical antagonism between individuals of the two species. This consideration is complicated by the probability that solitary fossorial forms display intraspecific antagonism. Interspecific antagonism would presumably surpass intraspecific antagonism in amplitude. If this is true

personatus appears to be the more formidable animal in deference to its larger body size. There is at least one point of supporting evidence. The contact locality of Skidmore is located near the union of sandy and semi-friable soils. The species *personatus* occupies the sandy region north of Skidmore but immediately south of Skidmore semi-friable soils are encountered and this species has pushed less than a mile into the area of adverse soils. The species *bursarius* occurs sporadically in this adverse region and was collected only two miles south of the site where *personatus* was collected. No intervening barriers are evident. It appears therefore that greater tolerance to clayey soils has permitted *bursarius* to range throughout the region south of Skidmore but the presence of *personatus* throughout the more favorable habitat of sand to the north has denied *bursarius* entry there. It appears that within a region of transitional environment these species with generally similar habitat preferences, though somewhat different tolerances, are reaching the periphery of the environment to which they are respectively adapted and are exerting pressure on one another in contact localities.

Discussion

Only in exceptional instances, such as the problem under study, where gene exchange between allopatric populations is apparently possible yet is minimal or lacking is it possible to observe the presence or absence of isolating mechanisms inherent in these allopatric populations. In mammals at least, analyses of populations dynamics in the field are more desirable and probably more reliable in determining fertility relationships and hence allopatric species validity than laboratory analyses with the accompanying, inevitable artificialities. Ordinarily evaluation of the evolutionary position of allopatric populations presents difficulty because it is rarely possible to determine the extent of reproductive isolation which has evolved; therefore, the assignment of specific or subspecific rank allopatric groups must often be arbitrary and reliance upon morphological criteria is necessarily preeminent. The seriousness of this difficulty is emphasized by the fact that morphological distinctness is not a reliable demonstration of the actuality of a species. A biological approach to species validity, on the other hand, is often applicable to related sympatric populations and occasionally permits even the delimitation of sibling species. Mayr (1942), Dobzhansky (1951) and others have pointed out that the evolutionary evaluation of sympatric populations is often clarified by evidence of effective reproductive isolation, such as coexistence or parapatry without gene exchange. In general, geographic races of allopatric populations and polymorphic groups within sympatric populations differentiate through similar agencies with the important difference that allopatric populations possess an added dimension, isolation. Most authors concur with the theory of allopatric rather than sympatric speciation representing the predominant evolutionary mechanism if not the sole mechanism (Mayr, 1947). One would expect allopatric races to diverge more rapidly than polymorphic sympatric groups and furthermore to be more highly adapted at any given time. In addition, non-adaptive modifications would tend to influence distinctiveness to a stronger degree in allopatric than in sympatric populations for in the latter non-adaptive characters would tend to reflect the consequence of intrapopulation gene exchange.

Evaluation of a series of closely related allopatric insular populations may be somewhat clarified by the occurrence of natural hybridization, often within a very localized area, as in the classic case of the New Guinea kingfisher, *Tanysiptera galatea* (Mayr, 1942), and certain of Darwin's Finches (Lack, 1947). Here reproductive isolation has not been fully attained in populations which have achieved marked morphological distinct-

ness. In these examples, however, confident evaluation is restricted to only the populations which are involved in the secondary intergradation. Clearly such cases are premature reunion of potential species but it does not necessarily follow that neighboring insular populations would behave similarly were they reunited. This is obvious for within any insular allopatric complex different stages of differentiation are invariably represented owing to the involvement of varying durations of isolation and varying mutations and selective pressures.

A parallel to the insular allopatric population problem is demonstrated in certain distribution patterns of continental populations. Some continental mammals are believed to have formerly enjoyed an extensive and generally areal distribution and more recently to have fractioned into disjunct units in response to significant climatic (and ecologic) changes, e.g., *Spilogale putorius* and *S. gracilis* (Blair, 1954), *Peromyscus maniculatus* and *P. polionotus* (Blair, 1951) and *Geomys bursarius* and *G. pinetis*. Under these circumstances effective isolation might be initiated at about the same time for several populations. This would seldom if ever obtain in an insular allopatric series since a group of animals would tend to invade islands one at a time. However, once an "insular" pattern of distribution has appeared, evaluation of each population's evolutionary status follows a similar approach whether the populations are continental or insular. The disruptive distribution pattern of the mountain pika, *Ochotona princeps,* is a pertinent example. This species manifests a highly disjunct boreal distribution which includes much of the Rocky Mountains of the western United States and southern British Columbia occupying principally high altitude talus situations up to 13,600 feet (Howell, 1924). Many of the numerous subspecies are confined to isolated areas of high elevation and several cases of intergradation between races were reported by Howell (*op. cit.*). This species exemplifies an intraspecific allopatric series of morphologically distinct populations with localized areas of intergradation. The essential point seems to be that where related forms exhibit geographically disjunct distribution, local intergradation may directly clarify evolutionary status of the involved populations but aid by inference only the evaluation of populations not involved.

In the majority of cases, allopatric species are separated spatially to such an extent that no opportunity arises in nature for contact. Here again the degree of reproductive isolation remains unknown. In some forms it is possible to derive helpful information through fertility tests in the laboratory but here another difficulty arises since some valid species will cross under laboratory conditions but apparently never in nature (Dobzhansky, 1951). Conversely, some mammals will not breed under artificial conditions even though they are of the same species, e.g., *Dipodomys ordi.* Laboratory mating-preference tests may render additional information as to reproductive isolation (Blair and Howard, 1944; Patterson, 1947; Dobzhansky and Koller, 1938). In these tests females (or males) are given opportunity to discriminate in choice of mates.

Infrequently the ranges of allopatric species of North American mammals approach one another and even effect a general region of approximation without significant overlap. However, this unusual relationship seems to occur always along lines of strong ecological breaks or contrasts. This situation is demonstrated by two species of cottontails: *Sylvilagus nuttalli* and *S. floridanus. S. nuttalli* occupies generally the western two-fifths of the United States and in the northern part of its range prefers sagebrush but in New Mexico occurs almost exclusively in timbered regions (Hall, 1951). *S. floridanus* ranges across the eastern three-fifths of the United States and is largely confined to riparian associations. Its range probably inter-

digitates to some extent with that of *nuttalli.* In New Mexico the ranges of the two species are generally in contact and Nelson (1909, 193) recorded a questionable hybrid. During isolation these species appear to have evolved differential habitat preferences but not complete reproductive isolation.

In several North American mammals the ranges of two related allopatric species adapted to habitats of different elevation approximate one another, e.g., the jack rabbits *Lepus californicus,* mostly under 7,500 feet, and *L. americanus,* 8,000 to 11,000 feet. A more striking example of this phenomenon is the case of the western pocket gophers *Thomomys talpoides* and *T. bottae* (Durrant, 1946). The northern species, *talpoides,* which prefers higher elevations reaches the southern limits of range in Utah. *T. bottae* prefers lower elevations and reaches the northern limits of range in Utah resulting in a line of contact which displays an intricate interdigitation of ranges. In the Oquirrh Mountains, Utah, an isolated population of *T. talpoides* is entirely surrounded by *T. bottae* occupying lower terrain. Here the occurrence of borderline areas between ranges of related allopatric species is clearly due to abrupt environmental contrast. Examination of the literature has revealed several borderline situations between the ranges of allopatric species of vertebrates but none involving two mammalian species with similar ecological requirements. However, Goldman (1947) reported that in southeastern Arizona the ranges of *Thomomys bottae* and *T. baileyi* interdigitate to some degree and these species apparently hybridize. Both species occupy principally plains and valleys in the lower portion of the Upper Sonoran Zone. This geographic relationship is yet poorly known and obscure and there is some question of the validity of these species. The phenomenon of interdigitation of ranges suggests some significant differential habitat preference. The approach of ranges of *G. personatus* and *G. bursarius* thus appears almost unique because of the similarity in ecological requirements and the lack of a conspicuous ecological break coincident with the contact zone.

Considering available avenues for dispersal, interspecific competition and habitat preferences and tolerances, some tentative conclusions may be drawn as to the distributional history of these species. *G. bursarius* displays an extensive distribution, occurring east, north and northwest of *personatus.* The present distribution of *personatus* in Texas is presumably Post-Pleistocene for this species has not been recorded from Texas Pleistocene faunas (*bursarius* has been recorded). It is possible that ancestral populations of *personatus* were forced southward along the northern Gulf coast of Mexico during glaciation in view of the fact that a relict population, *G. p. tropicalis,* occurs near Altamira, Tamaulipas, Mexico. No other population of *Geomys* occurs south of the Rio Grande River except a population of *G. a. arenarius* (Merriam, 1895) reported south of the river at El Paso, Texas. In view of the fact that *Geomys* has been recorded from Pleistocene faunas of southwestern Kansas (Hibbard, 1949), central Texas (*bursarius*; Follansbee, unpublished manuscript), and Nebraska (Schultz and Stout, 1948), it is reasonable to assume that ancestral populations of *bursarius* occurred north of *personatus* during glaciation. The geographic arrangement of the two species today lends corroboration to this point. Ancestral populations of *bursarius* probably occupied the region between the Nueces River and the San Antonio River prior to the arrival of ancestral *personatus* stock from the south. It is believed that *personatus* populations moved east by utilizing alluvial terraces of the upper reaches of several water-ways: the Aransas River, Medio Creek and Blanco Creek. This region consists generally of friable soils. The San Antonio River was reached at a point probably north of Riverdale.

South of Riverdale *bursarius* occurs today. Populations of *personatus* have pushed northward along the west bank of the San Antonio River at least as far as Falls City where today it is parapatric with *bursarius*. The fact that *personatus* has not crossed the San Antonio River seems to indicate that this species arrived along the west bank relatively recently.

Color measurements indicate that pelage color in *personatus* is more closely correlated with native soil color than is pelage color in *bursarius*. Assuming approximately equal selection pressure on each species, there seem to be two plausible although opposing interpretations of these results. First, these results might indicate that *personatus* is relatively stabilized in distribution and consequently high adaptive phenotypes have evolved, while *bursarius*, were this species extending its range, would manifest instability of phenotype. Another interpretation suggests that if *personatus* is assumed to be extending its range this species would be subjected to increased selective attrition as new habitats are encountered and only a restricted number of adaptive phenotypes would survive. Following this explanation *bursarius* color measurements would represent normal variation in color adaptation. Considering evidence that *personatus* has displaced *bursarius* in certain areas, the latter interpretation of color measurements is favored. In many localities where the ranges of these species approach one another, barriers of indurate soils (impediments to *personatus* at least) intervene. At Campbellton and Falls City *personatus* is presumably expanding its range northward at the expense of *bursarius*.

Summary

The biological dynamics of contact between the ranges of two allopatric species of pocket gophers, *Geomys personatus* and *G. bursarius*, in southern Texas were investigated. Ninety-one specimens of *G. bursarius* and 113 specimens of *G. personatus* were trapped. Field work proceeded irregularly between December 12, 1952 and April 6, 1955. The ranges of these two species approach one another at seven localities. At one trapping site both species were collected. No abrupt ecological changes coincide with the area of approximation between the ranges of the two species. Both species appear to have similar ecological requirements though different tolerances. Indurate soils are thought to constitute the most formidable barriers to dispersal in the area studied. Interspecific competition is thought to be largely responsible for separation of ranges. No evidence of hybridization or introgression was observed.

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Literature Cited

Aldous, C. M. 1951. The feeding habits of pocket gophers (*Thomomys talpoides moorei*) in the high mountain ranges of central Utah. J. Mamm., **32**: 84–87.

Blair, W. F. 1950. The biotic provinces of Texas. Tex. J. Sci., **2**: 93–117.

——. 1951. Interbreeding of natural populations of vertebrates. Amer. Nat., **85**: 5–30.

——. 1952. Mammals of the Tamaulipan biotic province in Texas. Tex. J. Sci., **4**: 230–250.

——. 1954. Mammals of the mesquite plains biotic district in Texas and Oklahoma, and speciation in the central grasslands. Tex. J. Sci., **6**: 235–264.

——, and W. E. Howard. 1944. Experimental evidence of sexual isolation between three forms of mice of the cenospecies *Peromyscus maniculatus*. Contrib. Lab. Vert. Biol. Univ. Mich., **26**: 1–19.

DAVIS, W. B. 1940. Distribution and variation of pocket gophers (Genus *Geomys*) in the southwestern United States. Tex. Agric. Exp. Sta. Bull., **590**: 1–38.

——. 1941. The moles (*Scalopus aquaticus*) of Texas. Amer. Mid. Nat., **27**: 380–386.

DOBZHANSKY, TH. 1951. Genetics and the origin of species. Columbia Univ. Press, New York. 1–364 pp.

——, AND P. C. KOLLER. 1938. An experimental study of sexual isolation in *Drosophila*. Biol. Zentralbl., **58**: 589–607.

DURRANT, S. D. 1946. The pocket gophers (Genus *Thomomys*) of Utah. Univ. Kansas Publ., Mus. Nat. Hist., **1**: 1–82.

FOLLANSBEE, L. A. 1951 (unpublished manuscript). A statistical study of two Pleistocene rodents from Texas. On file at the Texas Memorial Museum, Austin, Texas.

GOLDMAN, E. A. 1915. Five new mammals from Mexico and Arizona. Proc. Biol. Soc. Washington, **28**: 134.

——. 1947. The pocket gophers (Genus *Thomomys*) of Arizona. N. Amer. Fauna No. 59: 1–37.

HALL, E. R. 1951. A synopsis of the North American *Lagomorpha*. Univ. Kansas Publ., Mus. Nat. Hist., **5**: 119–202.

HIBBARD, C. W. 1949. Pleistocene vertebrate paleontology in North America. Bull. Geol. Soc. Amer., **60**: 1417–1428.

HOWELL, A. H. 1924. Revision of the American Pikas (Genus *Ochotona*). N. Amer. Fauna No. 47: 1–57.

INGLES, L. G. 1950. Pigmental variations in populations of pocket gophers. EVOLUTION, **4**: 353–357.

KENNERLY, T. E., JR. 1954. Local differentiation in the pocket gopher (*Geomys personatus*) in southern Texas. Tex. J. Sci., **6**: 297–329.

——. 1958. Comparisons of morphology and life history of two species of pocket gophers. Tex. J. Sci., **10**: 133–147.

LACK, D. 1947. Darwin's finches. Macmillan Co., New York. 1–208 pp.

MAYR, E. 1942. Systematics and the origin of species. Columbia Univ. Press, New York. 1–334 pp.

——. 1947. Ecological factors in speciation. EVOLUTION, **1**: 263–288.

MERRIAM, C. H. 1895. Monographic revision of the pocket gopher family *Geomyidae* (exclusive of the species of *Thomomys*). N. Amer. Fauna No. 8: 1–258.

NELSON, E. W. 1909. The rabbits of North America. N. Amer. Fauna No. 29: p. 193.

NORQUEST, C. E. 1941. Climate of the states (Texas). Agricultural Yearbook Separate No. 1860: 1129–1146.

PATTERSON, J. T. 1947. The insemination reaction and its bearing on the problem of speciation in the *mulleri* subgroup. Isolating Mechanisms, Univ. Tex. Publ., No. 4720: 41–77.

SCHULTZ, C. B., AND T. M. STOUT. 1948. Pleistocene mammals and terraces in the Great Plains. Bull. Geol. Soc. Amer., **59**: 553–588.

THARP, B. C. 1939. The vegetation of Texas. Tex. Acad. Sci. Publ. Nat. Hist., Nontech. Ser., **1**: 1–74.

THORNTHWAITE, C. W. 1948. An approach toward a rational classification of climate. Geogr. Rev., **38**: 55–94.

THORNTON, W. A., AND H. S. AL-UTHMAN. 1952. Pattern of distribution of the woodmouse in a part of the Texas Panhandle. Tex. J. Sci., **4**: 99–101.

VORHIES, C. T. 1945. Water requirements of desert animals in the Southwest. Univ. Arizona Tech. Bull., No. 107: 487–525.

WRIGHT, S. 1943. Isolation by distance. Genetics, **28**: 114–138.

EVOLUTION OF THE PSILOPHYTE PALEOFLORA

DANIEL I. AXELROD

University of California, Los Angeles 24

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INTRODUCTION

A century has now elapsed since Sir John William Dawson described the nude plant, *Psilophyton,* from the Devonian rocks of Gaspe (1859). Comprising an exceedingly ancient and simply constructed plant (fig. 1), it was the first fossil member of the ancient phylum Psilophyta to be discovered. At first the idea that it was a fossil plant was received with considerable scepticism but by the turn of the century, owing to the discovery of additional Devonian plants, it was generally conceded to be an authentic land plant. During the succeeding three decades numerous Devonian land plants of diverse character were described from rocks on all the continents. The problems of evolution posed by this earliest land vegetation—the Psilophyte Paleoflora—have been especially difficult to resolve. In particular, divergent views have been expressed with respect to their probable antiquity, their phylogenetic relations and their rate of evolution. Evidence afforded by more recent discoveries of new land plants in Devonian, Silurian and Cambrian rocks makes it possible to view these problems with better perspective. To understand the nature of the issues to be discussed, it is desirable first to recall certain salient features of the earliest land flora.

The oldest land plants now known are from the Early Cambrian of the Baltic region (Reissinger, 1939; Naumova, 1949), where approximately 20 spore-types of very simple construction in terms of size, shape, and sculpture are recorded. Spores of somewhat more complex character occur in the Middle and Late Cambrian of Kashmir, Spiti, and the Salt Range in India (Ghosh and Bose, 1950; 1952; Ghosh, Sen and Bose, 1951; Jacob *et al.*, 1953a; 1953b), and in eastern Sweden (Darrah, 1937). Approximately 60 Cambrian spore-genera are now on record, all discovered largely during the past decade.

These spores may be regarded as reproductive cells of land plants because they are cutinized. Further, at least some of the Cambrian plants were vascular since woody fragments showing scalariform tracheids, and tracheids with simple and bordered pits, occur in association with the spores in India. Most importantly, several phyletic lines appear to be represented, though their affinities in terms of modern types are difficult to judge. Naumova suggested that the spores from the Baltic region represent both Bryophyta and Pteridophyta. In the latter group she noted that one of the types is similar to spores of the *Calamariaceae* of Carboniferous age. The Indian workers (Jacob *et al.*, 1953b) report that their fossils apparently represent 6 different groups of vascular plants, chiefly primitive pteridophytes (including equisetalean types), probably seed ferns, and possibly primitive gymnosperms. That the phylum Lepidophyta was already established by the Middle Cambrian is shown by the occurrence of *Aldanophyton* in Siberia (Krystofovich, 1954), which is represented by several stems, one up to 8.5 cm. long, with spirally arranged microphyllous leaves.

Remains of land plants have not yet been recorded from Ordovician or Lower to Middle Silurian rocks. However, several genera are known from the Upper Silurian of Australia. Some are of un-

certain systematic position, others have been assigned to the Psilophyta, and one (*Baragwanathia*) is a well developed lycopod (Lang and Cookson, 1935). Commencing in the Early Devonian, vascular land plants are recorded in moderate numbers, and they increased in abundance and in diversity during the rest of the period. By Late Devonian time, the following major categories had become established:[1]

PSILOPHYTA ("psilophytes")
- Psilophytales (Rhynia, Psilophyton, Horneophyton, etc.)

LEPIDOPHYTA ("lycopods")
- Baragwanathiales (Baragwanathia)
- Protolepidodendronales (Protolepidodendron, Protolepidodendropsis)
- Lepidodendronales (Archaeosigillaria, Lepidodendron, Bergeria)

ARTHROPHYTA ("horsetails")
- Hyeniales (Hyenia, Calamophyton)
- Pseudoborniales (Pseudobornia)
- Sphenophyllales (Sphenophyllum)
- Calamitales (Asterocalamites, Calamites)

PTEROPHYTA ("ferns")
- Archaeopteridales (Archaeopteris)
- Protopteridales (Protopteridium, Iridopteris, Aneurophyton, Dawsonites, Reimannia)
- Coenopteridales (Clepsydropsis, Asteropteris)
- Cladoxyales (Cladoxylon)

PTERIDOSPERMOPHYTA ("seed ferns")
- Calamopityales (Calamopitys, Stenomyelon, Diichnia)

CONIFEROPHYTA ("conifers")
- Pityales (Callixylon, Paleopitys, Archaeopitys)

Three successive evolutionary phases have been described, including the Psilophyton Flora, the Hyenia Flora, and the Archaeopteris Flora, which lived in the Early, Middle and Late Devonian respectively. Named for one of the more typical genera of each association, these Floras largely represent different generic assemblages though some types occur in more than one Flora. In general, contemporaneous Devonian Floras from widely separated parts of the northern and southern hemispheres include many types in common. For this reason it has generally been supposed that the vegetation of the world showed essentially no regional differentiation during the Devonian (Seward, 1933; Dorf, 1955); as we shall see, however, important vegetation provinces were already in existence.

[1] Only a few examples of genera representing these orders are given here; some, of course, are monotypic.

Evolutionary Significance of Devonian Psilophytes

Interest in the Psilophyte Paleoflora has centered chiefly on the evolutionary significance of the most simple of known vascular plants, notably the "true" psilophytes of the Devonian, *Rhynia, Horneophyton,* and *Psilophyton.* The sporophyte of these plants consisted only of an upright axis that was adapted to life on land, including a simple vascular strand of phloem and xylem for conduction and support, stomata, cuticle, and cutinized spores: they were not differentiated into root, stem, and leaf (fig. 1). In basic morphology they are quite close to the hypothetical first land plants conceived by Lignier, Potonie, Bower, and Campbell, and serve as monuments to those superb morphologists and phylogenists who essentially described them before they were discovered.

As soon as these plants had been interpreted, chiefly on the basis of the remarkable silicified material in the Rhynie chert of Scotland (Kidston and Lang, 1917–21), it was only natural for most investigators to regard them as the actual ancestors of all higher vascular land plants. Since *Rhynia* was such a simply constructed plant (fig. 1), and closely agreed with the "prototype" of land plant which had been earlier visualized by Bower and others, it was quickly accepted

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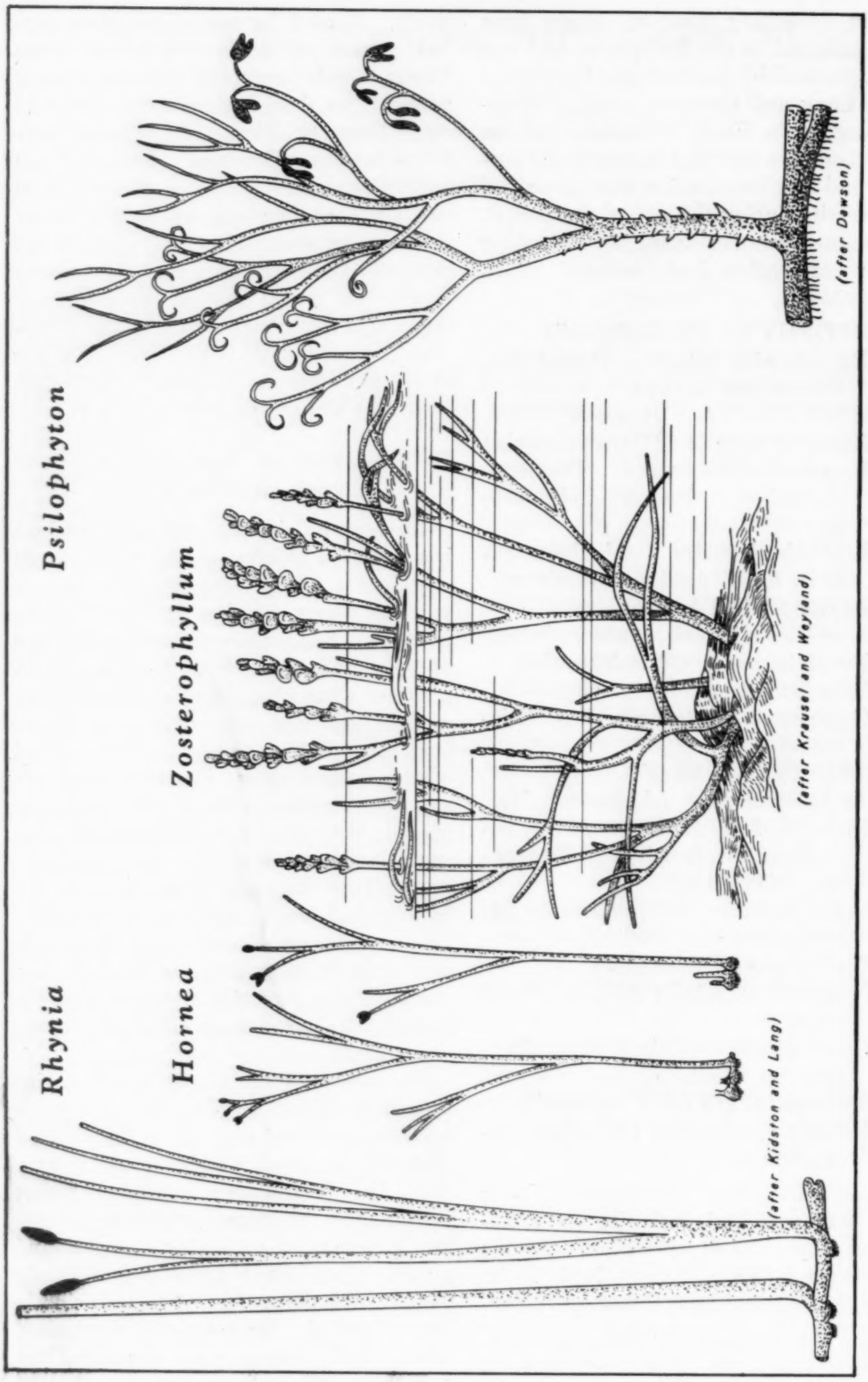

FIG. 1. Devonian psilophytes may only be bradytelic types persisting from the Precambrian.

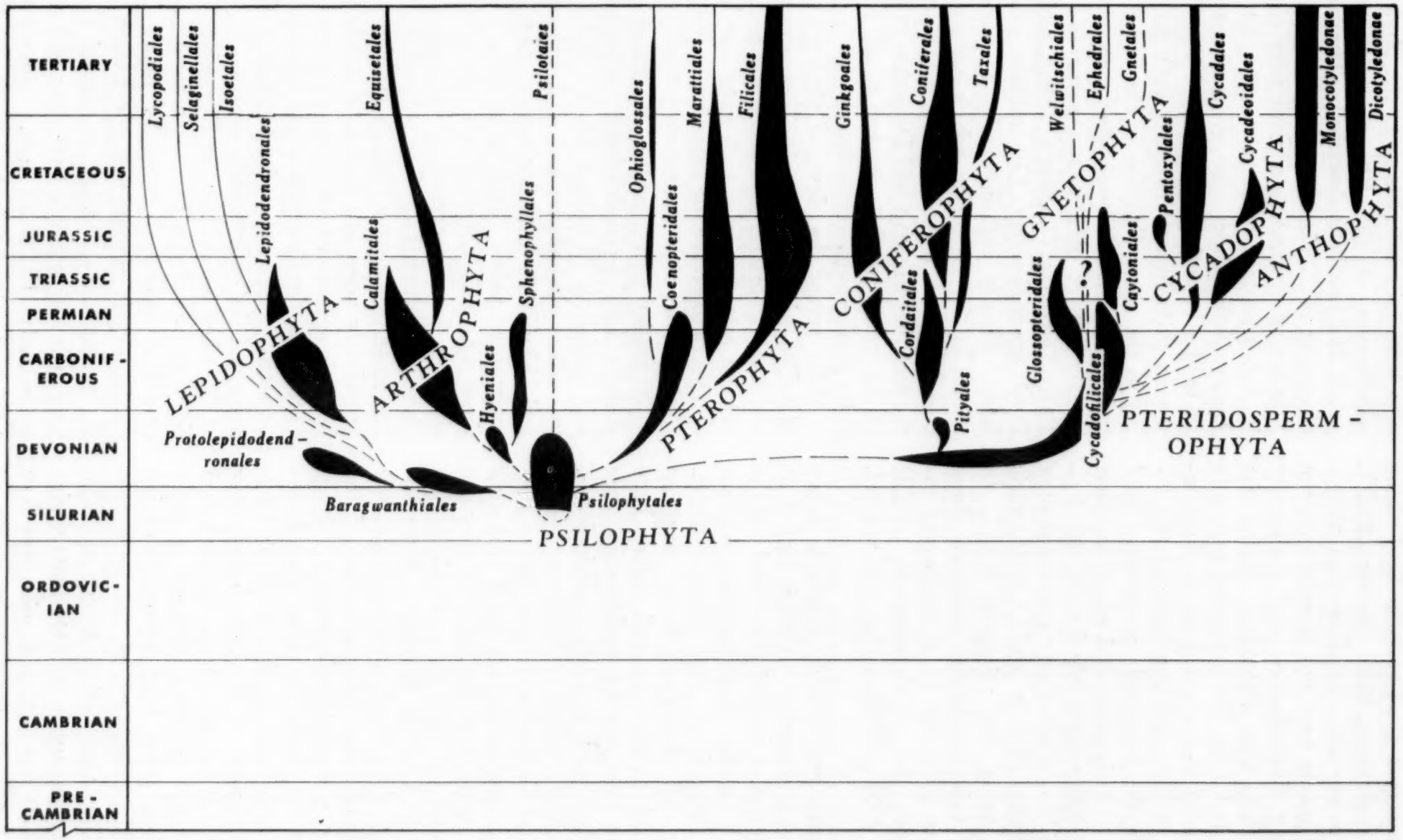

FIG. 2. Some investigators believe the Psilophyta occupied a central phylogenetic position during the Siluro-Devonian.

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as *the* ancestor of all vascular land plants (i.e. Zimmermann, 1930; Hirmer, 1927). Furthermore, since pre-Devonian vascular land plants were not then known, the increasing diversification and complexity of the Psilophyte Paleoflora during the Middle and Late Devonian led naturally to the belief that a great burst of evolutionary activity quickly followed the invasion of the previously unoccupied land (fig. 2). This presumed eruptive phase was believed responsible for the development of the successively more complex Psilophyton, Hyenia and Archaeopteris Floras (Arber, 1921; Seward, 1933). In spite of evidence to the contrary, these views are still held by a number of investigators i.e. Zimmermann, 1952; Smith, 1955; Takhtajan, 1956; Dorf, 1955).

Evidence was already available when *Rhynia* was described to show that it or other Devonian psilophytes could not be ancestral to the Lepidophyta, Arthrophyta, Pterophyta, and Coniferophyta. Actually, all living phyla of vascular plants had already evolved before Late Devonian time, except angiosperms (see list above) and possibly cycadophytes. The ancient conifers *Paleopitys* (descr. 1870) and *Callixylon* (descr. 1911) possessed complex secondary wood and were trees to judge from the fact that they are represented by logs: those of Callixylon were up to 3 feet in diameter. Most importantly, they lived contemporaneously with psilophytes. The existence of the lycopod *Protolepidodendron* (descr. 1880) in the Early Devonian should also have dispelled any doubts as to the phyletic significance of the psilophytes many years ago: if the psilophytes are ancestral (a point not proven), divergence must have taken place long before Devonian time. The discovery of the well preserved Devonian Gilboa forest in 1923, with *Aneurophyton* (*Eospermatopteris*) trees 25–40 feet tall and with 3–4 foot trunks that supported a large crown of fronds like those of tree ferns, should also have raised doubts as to the phyletic significance of the Rhynie psilophytes which had just been described. The later discovery of *Baragwanathia* in the Late Silurian of Australia—a plant very close in fundamental structure to the living *Lycopodium selago*—also gives us a clue as to the evolutionary status of the Devonian psilophytes. Another vane pointing in the same direction is the fact that the Cambrian *Aldanophyton* resembles certain species of *Drepanophycus* of the Early Devonian (Leclercq, 1956), which lived approximately 170 million years later. Finally, the discoveries of woody plants in the Cambrian which are more complex than *Rhynia* firmly establishes the fact that Silurian and Devonian psilophytes could not be ancestral to all vascular land plants.

If we accept the views of phylogenists of the *Rhynia*-school, notably Zimmermann and his supporters, then according to our present information it took over one billion years to evolve the structurally simple *Rhynia* from algal ancestors, yet only 15 to 20 million years (or less) to transform *Rhynia* into lepidodendrons, calamites, and cordaites, 75 million years (or less) to evolve cycadophytes and ginkgophytes, and 150 million years (or less) to develop magnolias, palms, and sycamores. To those who still construct phyletic charts showing the divergence of all vascular plant phyla from Late Silurian and Early Devonian psilophytes (fig. 2) we may appropriately point out that such a scheme is not in agreement with geologic evidence as to the antiquity of the phyla concerned, or with our present understanding of the nature of the evolutionary process.

The chief reason that the Devonian and Silurian psilophytes have been considered primitive, ancestral types by many investigators is simply that the nature of the evolutionary process, as viewed over long spans of geologic time, was still obscure only 15 years ago. Simpson's (1944; 1953) brilliant analysis of the tempo and mode of evolution, as based on

a synthesis of genetic and paleontologic data, has paved the way for a reappraisal of the early land plants. The true significance of the Silurian and Devonian psilophytes is to be found in our answer to the fundamental question which was earlier posed by Eames (1936), and more recently by others (Berry, 1945; Leclercq, 1954; 1955; Andrews and Alt, 1956): are the Devonian psilophytes archaic and ancestral, or are they only ancient, simple plants? There is now good evidence to show that they are ancient, simple plants which persisted long after their derivatives—*if any*—went on to explore other evolutionary avenues. They represent slowly-evolving (bradytelic) forms, types fully comparable to *Chara, Selaginella, Equisetum, Ginkgo, Araucaria, Marattia, Schizaea, Platanus,* and *Sassafras* in the plant kingdom, and to *Lingula, Limulus, Sphenodon, Didelphus,* and *Latimeria* in the animal world, all of which have persisted essentially unchanged for scores of millions of years (fig. 1).

The psilophytes were adapted to comparatively stable environments, chiefly the near-coastal swampy lowlands of a world in which the climate was mild into high latitudes during most of the Early and Middle Paleozoic, and probably earlier. Such an ecologic occurrence—in a geologically stable, common, and persistently widespread environment—explains readily the reported similarity of vegetation over the world in the Devonian (Seward, 1933; Dorf, 1955). However, we now know that plants which were transported into these lowland basins from the hinterlands comprised numerous forms that belonged to diverse vegetation types which were in the uplands, and further, these plants were more complex than those living in the lowlands which comprise the bulk of the record. The diversity and complexity of vegetation that existed in the continental interiors during the Devonian is indicated clearly by the rich spore floras which have now been described from Canada (Radforth and McGregor, 1954) and Germany (Thompson, 1952). The New Albany shale flora of the Kentucky-Indiana-Tennessee area (Hoskins and Cross, 1952) provides additional evidence. It comprises 30-odd genera, represented chiefly by wood transported by large rivers from the hinterland to a stagnant, lagoonal site of deposition. Numerous, highly complex types from the interior (including *Callixylon* logs) occur in association with the simple psilophytes which were chiefly of coastal swamp occurrence. Generally similar relations are shown also by the Devonian flora of Spitzbergen (Hoeg, 1942), and by a recently collected Devonian flora from east-central Nevada (UCLA coll.).

In these connections, it is pertinent to recall that the early Paleozoic plant record is much less complete than that of animals. This is chiefly because the hard parts of the recorded animal phyla are more readily preserved than are the leaves, seeds, or stems of plants. The great abundance and diversity of marine invertebrates in the early Paleozoic, as compared with the rarity of plants, is only a natural consequence of the record: it does not mean there were few or no plants. Those plants which may once have been preserved in continental sediments have largely been destroyed due to subsequent erosion, for nonmarine rocks do not last so long in the record as the marine. By contrast, the marine invertebrates lived at the sites of deposition which have been preserved. Furthermore, plants growing near the shores of the major geosynclines in which the bulk of the record accumulated had, in general, comparatively little hard tissue which would favor their preservation: the nearshore area in those times apparently was an ecologic refuge for ancient types which required continuously mild temperature to judge from their simple structure. More advanced forms with woody trunks and other hard parts were evolving prin-

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cipally in the more distant uplands, in areas of environmental diversity, and hence were so remote from the sites of deposition that most of them did not get into the lowland record, though occasionally some of them did (i.e. *Paleopitys, Callixylon*).

The fossil record thus supports the belief that the plants of the continental interiors were more highly evolved than the contemporaneous psilophytes which lived near the shore. The psilophytes were highly adapted to these lowland sites in which the environmental-organism relations were essentially unchanging, conditions now considered necessary for bradytelic lines (Simpson, 1944; 1953; Stebbins, 1950). The view that most Devonian lowland plants are relict types which express various experiments in different ways of life, and which evolved long before the Devonian, not only comes closer to the actual situation as judged from stratigraphic and phylogenetic evidence, but is consistent with current opinions as to the nature of the evolutionary process. On this basis we may conclude that the successive phases of the Devonian lowland vegetation, as recorded by the Psilophyton, Hyenia, and Archaeopteris Floras (Arber, 1921; Dorf, 1955), represent no more than the replacement of different ecologic units migrating from upland into lowland areas, and not evolutionary change as such. Analogous replacements are well documented for the Late Pennsylvanian (Elias, 1933), and also for the Tertiary as shown by the time-space relations of the Arcto-Tertiary, Neotropical-Tertiary, and Madro-Tertiary Geofloras (Chaney, 1947; Axelrod, 1939; 1958).

These interpretations give us a clue as to why the evolutionary relations of plants represented in the Devonian floras have become increasingly difficult to assess, as judged from the comments of various investigators (i.e. Hoeg, 1942; Andrews and Alt, 1956). The problem may be attributed partly to the fact that comparisons are being made between plants from lowland and upland areas which represent types in different ("primitive," "advanced") stages of evolution; further, some of those from the uplands represent members of lineages which had not previously been in the lowlands, and hence are wholly new to us (i.e. *Siderella*). In addition, part of the problem has been due to convergence in the evolution of the plant body in these ancient groups. We have thus been including in some of our taxa, such as *Psilophyton,* plants of diverse affinities (*see* Leclercq, 1954).

Since the Devonian land flora was composed of many plants, of which we have now examined only a few, and which represent diverse branches of several phyletic stocks, they could scarcely be expected always to provide evidence of types intermediate to previously known genera. Attempts to classify them into a so-called natural system would lead obviously to unsatisfactory results because during the adaptive radiation of major groups evolution leads to a phyletic branching so complex that any central line or trunk was essentially nonexistent. Since phyletic charts which have been assembled from ample paleontological data regularly suggest an evolutionary pattern more nearly resembling an intricately branched shrub—not a tall, sparsely branched tree—the inherent difficulties of placing accurately a series of disconnected twigs (fossils) in their proper position is apparent.

Precambrian Origins of the Land Flora

Since vascular land plants had already attained some diversity of type by the Early Cambrian, their earlier evolution must have taken place in Precambrian time. This brings up the problem as to whether the phyla of vascular plants evolved from the Psilophyta at that early date (or at any other time), or whether they have all had independent origins. In seeking an answer to this problem, we must remember that most authorities have assumed that the Tracheophyta (to which

these phyla belong) is a "natural" group: it is composed of plants having independent sporophytes with an open system of growth and vascular tissue. Is this sufficient to make it a "natural" alliance in terms of phylogenetic relations? (*also see* Bold, 1957). Has Nature been so rigid that vascular tissues evolved only once, and in only one line—the Psilophyta —from which the other phyla have diverged?

Actually, the record supports the belief that xylem and phloem elements may have developed repeatedly in different phyla, much like the cuticle, cutinized spores, heterospory, spines, seed habit, secondary wood, leaves or roots. It is pertinent that there are near-vascular Devonian plants which do not belong to any known phylum. *Crocalophyton,* a plant considerably larger and more complex than *Rhynia,* had a complex internal structure. Its apical meristem of indecisive character formed conducting cells that can be termed pre-tracheids. As Andrews and Alt (1956) have noted, had it evolved much further it would have given rise to a unique plant, and certainly one far removed from the simple *Rhynia. Nematophyton, Prototaxites* (3-foot trunks), and their relatives were near-vascular plants, with longitudinally aligned conducting cells. Their derivatives, if any, would also have been types quite unlike *Rhynia* which has been visualized as the prototype of all vascular plants. The great diversity of the psilophytes themselves, some of which (*Yarravia, Sciadophyton*) are far removed from *Rhynia,* also suggests that other evolutionary lines may have evolved vascular systems independently. Further, there are a number of genera which are often included provisionally in the psilophytes (i.e. *Schizopodium, Barinophyton, Gosslingia*) because they are "primitive types" that do not fall into any other group (*see* Arnold, 1947; Andrews and Mamay, 1955, for comments on morphology). They may well represent ancient stocks which are now extinct that developed vascular tissues independently of *Rhynia*: at least their morphology is sufficiently different in basic character to make their derivation from *Rhynia* seem most unlikely.

Such data make it probable that vascular tissue has evolved repeatedly in different phyla. This brings us back to the old question, which has been raised again in recent years (Eames, 1936; Berry, 1945; Andrews, 1947; Andrews and Alt, 1956), as to whether there were several transmigrations to land by plants of different basic alliances represented in an ancient, and largely extinct, algal plexus. Eames has rightly emphasized the fact that the variety of body type and sporangium position in the psilophytes is foreshadowed in the existing higher algae (Eames, 1936). No doubt there were many other novel algal types in earlier times, of which we have no record, that resembled psilophytes even more closely in these respects.

In this connection it is pertinent that although morphological studies suggest that such groups as the lycopods, arthrophytes and ferns are natural phyla, this is not true of the Psilopsida, a clear definition of which has not been achieved (*see* Leclercq, 1954, pp. 302–307). In general, those ancient, simple plants which do not fit well into the other phyla have been relegated to the psilophytes. Clearly, the evolutionary significance of the group cannot be resolved until we decide what the Psilophyta is in terms of accurate definition. If we confine to it *Rhynia* and *Horneophyton,* for example, and place the others in isolated groups of presently unknown affinity, then perhaps our ideas of morphology and evolution will at least express what we know. A clue as to how we might then view the psilophytes is provided by examples of the evolutionary history of certain living plants. The present day *Isoetes* apparently culminates the reduction series *Sigillaria-Pleuromeia-Nathorstiana-Isoe-*

Mamay, 1955, for comments on morphol-

tites-Isoetes which extends down into the Carboniferous, a span of some 300 million

years. Since the history of vascular plants ranges into the Precambrian, fully 200 million years below the Devonian, is there any reason why some of the Devonian psilophytes are not reduced, simplified members of ancient lines? The living *Selaginella* and *Lycopodium* are essentially unchanged from the related *Selaginellites* and *Lycopodites* of the Carboniferous. The *Aldanophyton-Drepanophycus* line of evolution appears to be another example of a bradytelic line (Leclercq, 1956, p. 112), persisting from the Middle Cambrian into the Devonian. May not some psilophytes also represent bradytelic types of ancient isolated lines which largely became extinct in the Devonian? The cycadeoids and caytonias were large, diversified groups which died out in the Early Cretaceous. Is it not possible that some psilophytes comprise the last members of more ancient stocks which earlier in their history also were highly diversified, though comparatively primitive plants? And if vascular plants have had diverse sources in the algae, can not some of our "problem" psilophytes represent members of ancient, isolated, small phyla which have long been extinct?

Perhaps we have been too inclined to stuff all "primitive" land plants into the Psilopsida. Although most investigators are now agreed that the group is "unnatural," let us remember that Nature did not make it so. May we not be on sounder grounds from an evolutionary viewpoint if we entertain more seriously the possibilities that (1) all the phyla of vascular plants may extend back through a general "psilophytic stage" to independent (and unknown) algal sources (fig. 3), and that (2) other phyla of plants which are now extinct may also have included psilophytic plants. On this basis, the Psilophyta as now conceived may represent an ancient group of *unrelated* plants in various primitive ("psilophytic") stages of evolution which developed from diverse algal alliances. Since all phyla of vascular plants have passed through a primitive stage, then it must follow that all of them at some time have been "psilophytic"; but it does not follow that they were all derived from psilophytes.

Time of Transmigration

One problem that has been frequently raised is: Why did it "take so long" for plants to transmigrate from sea to land (Andrews and Mamay, 1955)? Actually, there is no concrete evidence to suggest that it did. The problem lies partly in understanding the nature of the record. The bulk of the unmetamorphosed Lower Paleozoic and Precambrian sedimentary section now available for study is marine, not continental: hence few records of land plants would be expected in it. Whilst they may once have been preserved in the nonmarine section, most of it has been eroded and the record is lost. Judging from the inferred nature of Cambrian land plants, the late Proterozoic land flora may have been nearly as complex as that which has been preserved in the Late Silurian to Middle Devonian rocks. But rather than being in the low lands, it probably was in the more distant uplands of environmental diversity, areas propitious for rapid evolution. Pertinently, plants in general seem to have evolved in much the same manner as animals, at least in terms of the broader aspects of tempo and mode (Stebbins, 1952). As Simpson has shown, the major phyla of vertebrates—"fishes," amphibia, reptiles, birds, mammals—took on the order of 40 to 50 million years to evolve from their respective ancestral types. Modern ferns, cycadophytes, and angiosperms required fully as long to diverge from their earlier forerunners (Axelrod, 1952). From his critical researches on the evolution of the coniferophytes, Florin (1949) has concluded that the Cordaitae, Ginkgoinae, Coniferae and Taxineae probably were already distinct by the Late Devonian-Mississippian. This suggests the ancestry of the group probably extends into the Silurian. Further, the occurrence of coniferous trees with 3-foot trunks (i.e. *Callixylon*) in the

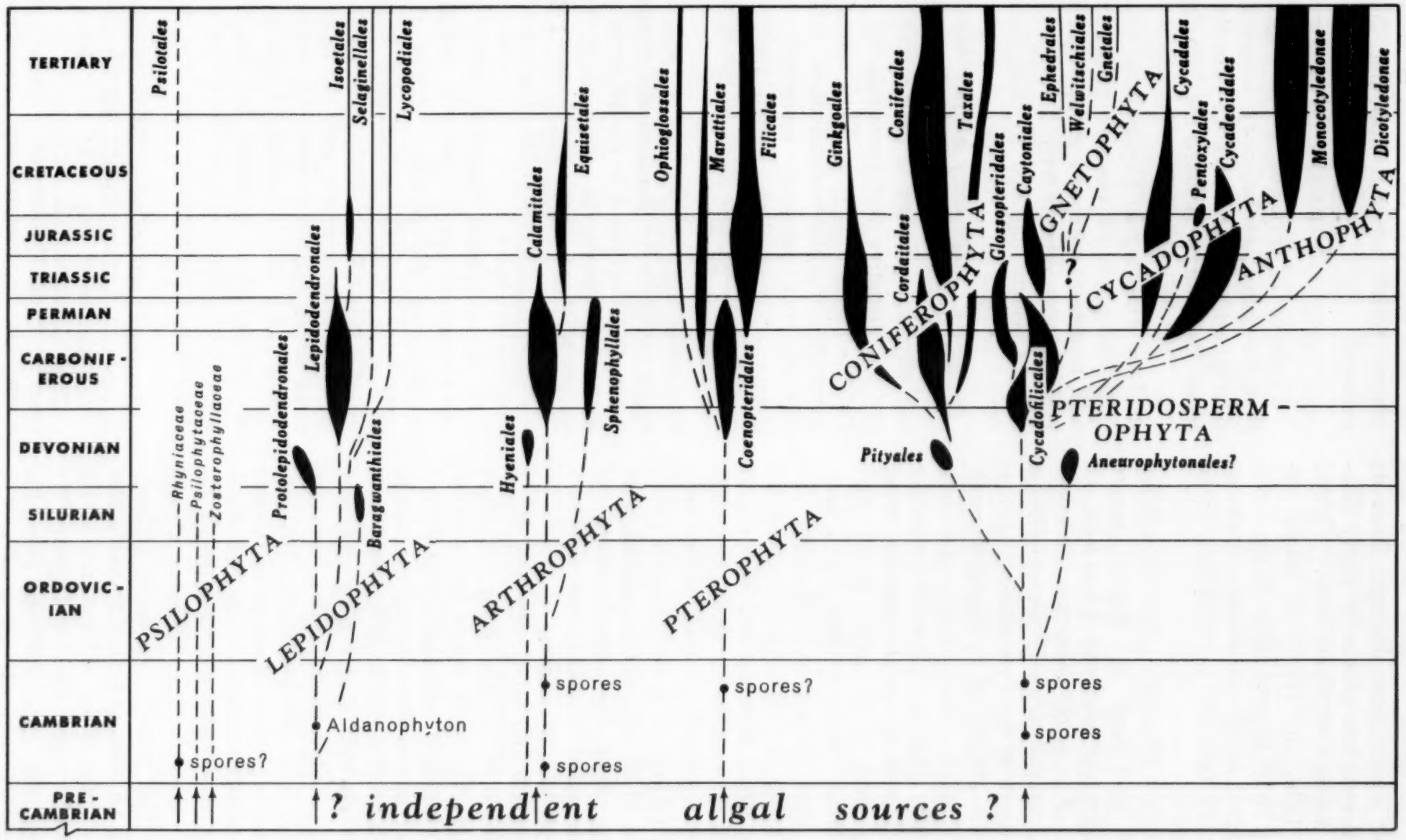

FIG. 3. Increasing evidence suggests that these plant phyla probably had independent algal sources (*cf.* fig. 2).

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Middle Devonian probably means that the basic conifer type diverged from its ancestral seed-fern plexus by Early Silurian, if not in Ordovician time. Viewed in this light, the report of spores resembling those of seed ferns in the Cambrian is not at all surprising (Andrews and Alt, 1956, p. 365), but is fully to be expected.

The future discovery of a Precambrian vascular land flora of complex nature should therefore not amaze us, at least not in terms of its actual existence. It would appear that the times of transmigration fall far down in the Precambrian because algae were already in existence approximately a billion years prior to the Cambrian. The great morphological diversity of algae is well recognized, and they most probably were quite varied in the later Precambrian. If we assume that a number of algal groups were invading the lands during the Precambrian, then the apparent great diversity and high degree of organization of the Cambrian land flora is readily accounted for, and the Devonian psilophytes become ancient, slowly-evolving types of diverse alliances which were persisting in a "psilophytic stage" of evolution, some of which may be members of phyla now extinct.

These facts and inferences lead to the suggestion that our view of the Psilophyte Paleoflora has been much too narrow. As we bring early land plants into sharper focus in terms of their geologic, ecologic, and evolutionary relations, it seems clear that our phyletic charts need extensive revision, possibly on the order suggested here (fig. 3). Obviously, no final answers can be given to these problems that still surround the origins of the Psilophyte Paleoflora, and they will be with us for years to come. They deserve careful consideration from a broadened outlook, and with an open system of thinking that can only come when we are free of the shackles of a rigid phyletic dogma. We may hope that new evidence from the Cambrian, and from the still older, and as yet undiscovered, land plants of Precambrian time will illuminate more clearly the early history of the terrestrial flora, a history which we can now but dimly perceive.

Summary

Evidence is reviewed which suggests that the salient evolutionary features of the earliest vascular land flora—the Psilophyte Paleoflora—included the following:

1. The Psilophyte Paleoflora was already in existence in Precambrian time.
2. The phyla of vascular plants may well represent unrelated groups that developed independently from different algal sources which migrated to land during the Precambrian, passing through a "psilophytic" stage early in their history.
3. The Late Silurian and Devonian psilophytes, and many of their associates, are not primitive and ancestral, but are ancient bradytelic types. They comprise members of different alliances which probably had persisted essentially unchanged since the Precambrian, surviving in mild, lowland sites close to sea level.
4. The reported similarity of vegetation across the earth during the Devonian applies only to the floras of the swampy lowlands. Vegetation in the adjacent uplands was diverse in composition, and largely included plants which were morphologically far advanced beyond the simple psilophytes.
5. The presumed "rapid evolution" of the Devonian flora is due to a misinterpretation of the record. Rather than comprising successive evolutionary stages, the Psilophyton, Hyenia, and Archaeopteris Floras represent only the replacement of lowland by more highly adapted upland floras which had evolved in areas of environmental diversity far removed from the lowlands where the record accumulated, and long before the Devonian.

Literature Cited

Andrews, Jr., H. N. 1947. Ancient plants and the world they lived in. Comstock Publ. Co., New York. 279 pp.

——, and S. H. Mamay. 1955. Some recent advances in morphological paleobotany. Phytomorphology, **5**: 373–393.

——, and Karen S. Alt. 1956. *Crocalophyton:* a new fossil plant from the New Al-

bany shale, with some comments on the origin of land vascular plants. Ann. Missouri Bot. Gard., **43**: 355–378.

ARBER, E. A. N. 1921. Devonian floras. Cambridge Univ. Press. 109 pp.

ARNOLD, C. A. 1947. An introduction to paleobotany. McGraw-Hill Book Co. 433 pp.

AXELROD, D. I., 1939. A Miocene flora from the western border of the Mohave desert. Carnegie Inst. Wash. Pub. 516.

——. 1952. A theory of angiosperm evolution. EVOLUTION, **6**: 29–60.

——. 1958. Evolution of the Madro-Tertiary Geoflora. Bot. Rev., **24**: 433–509.

BERRY, E. W. 1945. The beginnings and history of land plants. Johns Hopkins Univ., Studies in Geol., **14**: 9–91.

BOLD, H. C. 1957. Morphology of plants. Harper & Bros. 699 pp.

CHANEY, R. W. 1947. Tertiary centers and migration routes. Ecol. Monogr., **17**: 139–148.

DARRAH, W. C. 1937. Spores of Cambrian plants. Science, n. s., **86**: 154–155.

DAWSON, J. W. 1859. On fossil plants from the Devonian rocks of Canada. Geol. Soc. London, Quart. Jour., **15**: 477–488.

DORF, E. 1955. Plants and the geologic time scale. *in* The Crust of the Earth. Geol. Soc. Amer. Spec. Paper 62: 575–592.

EAMES, A. J. 1936. Morphology of vascular plants: Lower groups. McGraw Hill Book Co. 433 pp.

ELIAS, M. K. 1933. Late Paleozoic plants of the Midcontinent region as indicators of time and of environment: Internat. Geol. Congr., Report of 16th session, U.S.A., **1**: 691–700.

FLORIN, R. 1949. The morphology of *Trichopitys heteromorpha* Saporta . . . . Acta Horti Bergiani, **15**: 79–109.

GHOSH, A. K., AND A. BOSE. 1950. Microfossils from the Cambrian strata of the Salt Range, Punjab. Trans. Bose Res. Inst., **18**: 71–78.

—— AND ——. 1952. Spores and tracheids from the Cambrian of Kashmir. Nature, **169**: 1056–1057.

——, J. SEN AND A. BOSE. 1951. Evidence bearing on the age of the Saline Series in the Salt Range of Punjab. Geol. Mag., **88**: 129–132.

HIRMER, M. 1927. Handbuch der Palaeobotanik. 708 pp. Munich.

HOEG, A. O. 1942. The Downtonian and Devonian Flora of Spitzbergen. Norges Svalbard.-OG Isharvs-Undersokelser, Oslo, 1–228.

HOSKINS, J. H., AND A. T. CROSS. 1952. The petrification flora of the Devonian-Mississippian black shale. The Paleobotanist, **1**: 215–244.

JACOB, K., MRS. CH. JACOB AND R. N. SHRIVASTAVA. 1953*a*. Evidence for the existence of vascular land plants in the Cambrian. Current Sci., **22**: 34–36.

—— AND —— AND ——. 1953*b*. Spores and tracheids of vascular plants from the Vindhyan System, India: the advent of vascular plants. Nature, **72**: 166–167.

KIDSTON, R., AND W. H. LANG. 1917–21. Old Red Sandstone plants showing structure from the Rhynie chert bed, Aberdeenshire, pts. I–V. Roy. Soc. Edinb., Trans., 51–52.

KRYSTOFOVICH, A. N. 1954. Discovery of lycopodiaceous plants in the East-Siberian Cambrian. Dokladi Akad. Nauk U. S. S. R., **91**: 1377–1379. (*in* Russian)

LANG, W. H., AND I. C. COOKSON. 1935. On a flora including vascular land plants associated with *Monograptus* in rocks of Silurian age from Victoria, Australia. Phil. Trans. Roy. Soc. London, ser. B, **224**: 421–449.

LECLERCQ, S. 1954. Are the Psilophytales a starting or a resulting point? Svensk Bot. Tidskrift, **48**: 301–315.

——. 1955. Evidence of vascular plants in the Cambrian. EVOLUTION, **10**: 109–114.

NAUMOVA, S. N. 1949. Spores of the Lower Cambrian. Bull. Acad. Sci. U. S. S. R., **4**: 49–56. (trans. from Russian)

RADFORTH, N. W., AND D. C. MCGREGOR. 1954. Some plant microfossils important to Pre-Carboniferous stratigraphy and contributing to our knowledge of the early floras. Canadian Jour. Bot., **32**: 601–621.

REISSINGER, A. 1939. Die "Pollenanalyse" Angedehnt auf alle Sedimentgesteine der geologischen Vergangenheit. Paleontographica, B, **84**: 1–20.

SEWARD, A. C. 1933. Plant life through the ages. Cambridge Univ. Press. 607 pp.

SIMPSON, G. G. 1944. Tempo and mode in evolution. Columbia Univ. Press. 237 pp.

——. 1953. The major features of evolution. Columbia Univ. Press. 434 pp.

SMITH, G. M. 1955. Cryptogamic botany. v. 2. Bryophytes and Pteridophytes. McGraw-Hill Book Co. 399 pp.

STEBBINS, JR., G. L. 1950. Variation and evolution in plants. Columbia Univ. Press. 643 pp.

TAKHTAJAN, A. L. 1956. Telomophyta 1. Psilophytales-Coniferales. Academia Scientiarum U. S. S. R., Instit. Botanicum. 488 pp.

THOMPSON, P. W. 1952. Beitrag zur Kenntnis der Sporomorphenflora im Unter- und Mitteldevon. Paleont. Z., **25**: 155–159.

ZIMMERMANN, W. 1930. Phylogenie der Pflanzen. Jena.

——. 1952. Main results of the "Telone Theory." The Paleobotanist, **1**: 456–470.

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NOTES AND COMMENTS

CHROMOSOMAL ABERRATIONS IN *PODOPHYLLUM PELTATUM*

LESTER J. NEWMAN [1]

Department of Zoology, Washington University, St. Louis 5, Missouri

Podophyllum peltatum (May Apple or Mandrake), a clonal perennial woodland herb of Eastern North America, is characterized by an underground rhizome system and flowering stems with two shield-shaped leaves and a solitary white flower between the leaves. Meiosis in *P. peltatum* has been described by Mottier (1907) using paraffin sections and Kaufmann (1926) using paraffin sections and iron alum haematoxylin smears. Darlington (1936) describes the meiosis of another species, *Podophyllum versipelle*. No mention is made of any meiotic irregularity in the papers on *P. peltatum*. Darlington describes one case of an acentric fragment found in the mitosis of the pollen grain. He regards this as evidence for crossing over within an inversion. The purpose of this paper is to present observations of chromosome aberrations as observed during meiosis in *P. peltatum*.

Clones of *P. peltatum* located in three native woodland areas in the City of St. Louis and St. Louis County, Missouri, were selected for study. Areas A and B, located in St. Louis County, are separated by 2 miles. Area D is located in Forest Park, City of St. Louis, 11 miles from areas A and B. Flower buds were collected from two clones in area A, two clones in area B, and seven clones in area D. Meiosis of pollen mother cells occurred from 10 to 16 April in the spring of 1958. Selection of buds at any given stage is difficult since there is little syncronization between plant size and meiotic stage. Data for certain stages are therefore missing from a number of clones.

Flower buds were fixed in the field in 1:3 acetic-alcohol and stored in 70% alcohol. Observations were made with temporary squash preparations of anthers using 1% acetic-lacmoid for the tetrad stage and 1% acetic-orcein for the other meiotic stages.

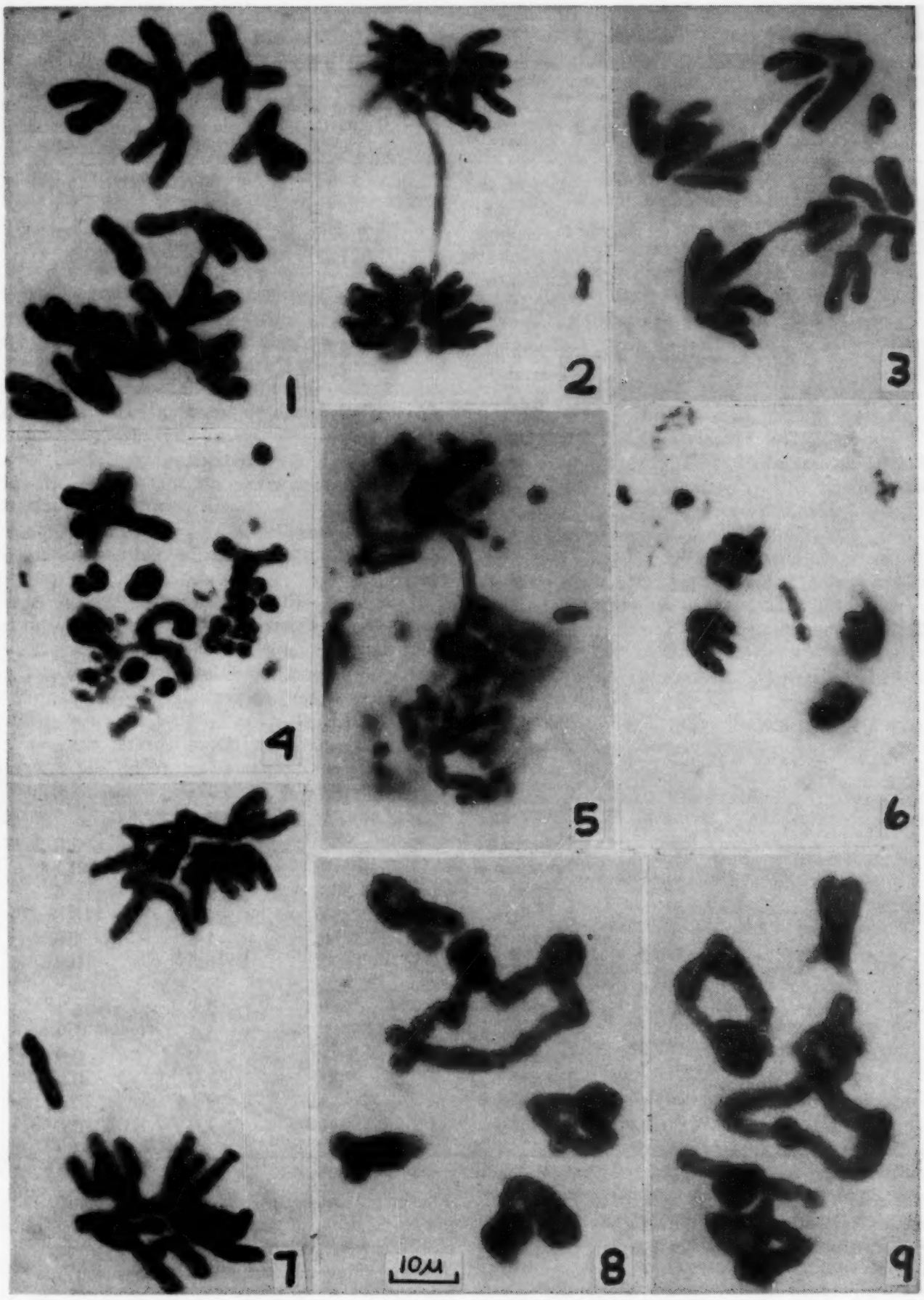
Podophyllum peltatum has a haploid chromosome number of six as determined through a study of meiotic figures. There are two metacentric, two submetacentric, and two telocentric chromosomes. The first identifiable stage is pachytene. In the diplotene stage chiasmata are present in all tetrads. Chromosomes of both pachytene and diplotene stages are quite tangled and are therefore difficult to analyse. Six tetrads exhibiting varying degrees of chiasma terminalization become aligned on the equatorial plate in the first division metaphase. The chromatids in anaphase I move towards their respective poles in a regular manner except for several cases where there seems to be difficulty in the separation of one or two pairs of chromatids. A distinct interphase stage follows during which the chromosomes lose their identity and form a typical resting nucleus. During prophase II the chromosomes again regain their identity. Metaphase II and anaphase II occur quite normally with cell walls forming around the four daughter nuclei in the tetrad stage.

Pollen mother cells with a dicentric chromatid bridge and an acentric fragment (figs. 1, 2, and 3) were common to all clones in which anaphase and telophase figures were found as indicated in table 1. The bridge, which in some cases becomes quite thin at the metaphase plate, may break during telophase I or persist through interphase into the second meiotic division, finally breaking in the formation of the tetrad stage. The fragment, which is usually found between the two sets of anaphase chromatids, is frequently the size of one arm of a metacentric chromatid. The fragment varies from U to rod-shaped. Second division bridge and fragment figures (fig. 3) were observed in clones with anaphase and telophase II stages. The following data were obtained in a detailed analysis of 525 anaphase I figures of clone B2: 10.6% first division bridge and fragment, 5.9% second division bridge and fragment, 7.6% one or two fragments, 2.3% extreme fragmentation.

Chromosome fragmentation, which occurs in all clones, appeared in two forms: extreme fragmentation (figs. 4 and 5) resulting in five or more fragments per cell and a less extreme type of fragmentation (figs. 6 and 7) wherein one and rarely two fragments per cell appear. The extreme fragmentation was observed in all of the pollen mother cells of two flower buds of clone B1 and in small numbers in the other clones. This type of fragmentation was observed in all meiotic stages, however in many cases the meiotic stage was obscured by the fragmentation.

The frequency of pollen mother cells with one or two fragments but no bridge is indicated

[1] Present address: Department of Zoology, University of Michigan, Ann Arbor, Michigan.



FIGS. 1–9. Acetic-orcein squash preparation of *P. peltatum* pollen mother cells. All figures to same scale. 1. Anaphase I bridge and fragment. 2. Telophase I bridge and fragment. 3. Anaphase II second division bridge and U-shaped fragment. 4 and 5. Extreme fragmentation. 6. Telophase II single fragment. 7. Telophase I single fragment. 8. Metaphase I ring of four chromosomes and four tetrads. 9. Metaphase I catenated ring of four chromosomes and four tetrads.

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TABLE 1. *Chromosomal aberrations in pollen mother cells of nine clones of* Podophyllum peltatum *collected in the vicinity of St. Louis, Missouri*

Location	Clone designation	Stage	Total no. PMC counted	Per cent cells with one or two fragments	Per cent cells with first division bridge and fragment
St. Louis County	B1	Anaphase I	34	0.0	17.6
		Telophase I	57	7.0	3.5
		Interphase	328	1.5	0.9
		Prophase II	126	1.6	2.4
		Anaphase II	18	16.6	5.6
		Tetrad	5250	1.0	0.0
	B2	Anaphase II	525	7.6	10.6
		Tetrad	597	10.9	0.0
City of St. Louis	D1	Anaphase I	164	4.9	11.6
		Telophase I	153	11.8	6.5
		Interphase	283	9.9	1.1
		Prophase II	339	2.4	2.7
		Anaphase II	242	3.3	6.7
		Tetrad	1992	3.1	0.6
	D2	Anaphase I	50	2.0	6.0
		Telophase I	18	5.3	5.3
		Interphase	56	5.4	0.0
		Prophase II	34	5.9	2.9
		Tetrad	1100	7.7	0.0
	D3	Telophase II	64	0.0	7.8
		Tetrad	800	0.8	0.0
	D4	Tetrad	1100	0.5	0.0
	D5	Telophase I	67	11.9	3.0
		Interphase	149	11.4	0.7
		Prophase II	500	4.6	4.4
		Anaphase II	83	1.2	18.8
		Telophase II	55	1.8	1.8
		Tetrad	1000	6.5	0.0
	D6	Anaphase I	141	2.8	6.4
		Telophase I	211	6.2	1.9
		Interphase	103	2.9	0.0
		Tetrad	200	4.0	0.0
	D7	Tetrad	400	2.0	0.0

in table 1. The fragments appear in the tetrad stage as micronuclei, both in the cytoplasm of the microspore or with their own cytoplasm and cell walls.

Another figure indicating chromosomal aberration was found in metaphase I where there were four normal tetrads and a circle or catenated ring of four chromosomes in each pollen mother cell (figs. 8 and 9). One metacentric and one submetacentric tetrad were involved in the configuration. Metaphase figures were found in seven of the eleven clones examined. The circle configuration was found in all metaphase figures of clones A2 and D1. These clones are separated by eleven miles.

The bridge and fragment aberration may be interpreted to indicate the presence of an inversion. However the details of the inversion: its length, form taken in pachytene and the chromosome involved, are still unknown. It should be noted from table 1 that data indicating the presence of the inversion are limited to seven of the nine clones studied. It is possible of course that some or all of the bridge

and fragment figures may be due to breakage-fusion-bridge cycles rather than an inversion. This is suggested by the U-shaped fragments and the second division bridge and fragments. The present technique does not allow detailed examination of pachytene figures which may or may not reveal inversion loops necessary for positive identification of an inversion.

Fragmentation exists in two clearly defined forms. The extreme form of fragmentation results in complete meiotic failure. The less extreme fragmentation of one or two fragments per pollen mother cell apparently does not disrupt meiosis but produces pollen with chromosome deficiencies. It is possible of course that some of these fragments arise from bridge and fragment figures in which the bridge has broken, but are far too numerous for this to be considered the only cause.

The circle and catenated ring configuration indicates that two of the seven clones showing metaphase I figures are heterozygous for a reciprocal translocation. One metacentric and one submetacentric tetrad are involved in the translocation.

It is interesting to note that the chromosomal aberrations of two types of fragmentation and bridge and fragment figures as reported here in *P. peltatum* are strikingly similar to those found in *Paeonia californica* and *brownii* as recently reported by Walters (1956, 1958).

There are certain limitations in the data presented in this paper. The critical anaphase and telophase stages do not occur in sufficient numbers for an accurate indication of aberration frequency. A detailed study of the aberrations, especially in the earlier meiotic stages is also necessary for more accurate data. A more detailed description of the chromosomal aberrations of *Podophyllum peltatum* will be presented in future papers.

Summary

Chromosomal aberrations indicating the presence of inversion, two types of fragmentation, and a translocation, were observed in a study of meiosis in pollen mother cells of the plant *Podophyllum peltatum* collected in St. Louis, Missouri, during the spring of 1958.

Literature Cited

Darlington, C. D. 1936. The analysis of chromosome movements. I. *Podophyllum versipelle*. Cytologia, **7**: 242–274.

Kaufmann, B. P. 1926. Chromosome structure and its relation to the chromosome cycle. II. *Podophyllum peltatum*. American Journal of Botany, **13**: 355–363.

Mottier, D. M. 1907. Development of the heterotypic chromosomes in pollen mother cells. Annals of Botany, **21**: 309–345.

Walters, J. L. 1956. Spontaneous meiotic chromosome breakage in natural populations of *Paeonia californica*. American Journal of Botany, **43**: 342–354.

Walters, J. L. 1958. Translocation heterozygosity in natural populations of *Paeonia brownii*. Proc. X Inter. Congr. Genet., Vol. II: (abstracts) 306–307. Univ. Toronto Press, Toronto, Canada.

IS *HORDEUM AGRIOCRITHON* THE ANCESTOR OF SIX-ROWED CULTIVATED BARLEY?

Daniel Zohary

Department of Botany, The Hebrew University, Jerusalem, Israel

In 1938 Åberg reported his finding of a brittle six-rowed barley in collections obtained from Tibet. He described this form (Åberg, 1938, 1940) as a new wild species—*Hordeum agriocrithon*—and considered it as the wild progenitor of six-rowed cultivated barley. Although only few seeds of this form have been obtained and natural populations of *H. agriocrithon* have not been observed, the existence of this form as a genuine wild species has been widely accepted by students of barley. In most phylogenetic schemes, which have been advanced in the last twenty years to account for the evolution of cultivated barley (for details see reviews by Schiemann, 1948, and by Takahashi, 1955), *H. agriocrithon* is considered as the starting step for the formation of cultivated, six-rowed *H. vulgare*.

Brittle six-rowed barley plants, morphologically identical with Åberg's *H. agriocrithon*, have also been reported by Kamm (1954) from Israel. In the last three years they have been repeatedly encountered by the present author in this country. However, examination of their distribution and ecology revealed the striking feature of their almost exclusive association with natural hybrid swarms between cultivated six-rowed barley *H. vulgare* and the wild, brittle, two-rowed *H. spontaneum* Koch (= *H. ithaburense* Boiss.).

Wild *H. spontaneum* is widely spread over central and northern Israel. It is especially

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common in eastern Galilee (east of a line drawn from Safad to Mount Tabor). In the semi-steppe herbaceous shrub formations which are predominant in this area, *H. spontaneum* is one of the most important annual grass constituents. This wild barley is also very common in Hartuv-Beit Guvrin area in the foothills of the Judaean Mountains. Hybrid swarms between wild *H. spontaneum* and cultivated six-rowed *H. vulgare* have been frequently and repeatedly encountered in these areas. As in many other cases of interspecific hybridization (Anderson, 1953), these swarms always occur in disturbed habitats such as recently abandoned fallow fields, edges of cultivated land and roadsides. They are always found in close proximity to pure *H. spontaneum* populations which occupy the adjacent undisturbed hillsides. More than thirty such hybrid swarms have been examined. The majority of them were found to contain a whole range of intermediates and recombinants between *H. spontaneum* and *H. vulgare*. Plants morphologically identical with *H. agriocrithon* occurred frequently in these hybrid swarms but always among other recombinations and intermediate forms.

These facts raise serious doubts as to the validity of *H. agriocrithon* as a genuine wild species. To these one has to add the results obtained by Kamm when he grew progeny from several *H. agriocrithon* plants collected by him in Israel. Progeny of some of these plants (Kamm, 1954, and personal communication) segregated for the several diagnostic characters which separate this form from *H. spontaneum* and *H. vulgare* (e.g. brittleness vs. nonbrittleness; two rows vs. six rows); several other *agriocrithon* plants bred true. This is exactly what one would expect of hybrid derivatives in a group where self-pollination predominates. Fixation of intermediates or recombination forms should be achieved here quite rapidly when such forms survive.

Another point that should be considered is the biology of seed dispersal of *H. spontaneum* as compared to *H. agriocrithon*. The sharp, narrow, spearlike, one-seeded dispersal unit of *H. spontaneum* is well adjusted to the open steppe or steppe-like conditions under which this annual grass grows. Immediately after ripening and disintegration of the ear, these units fall head down to the ground and become firmly anchored in soil cracks and in organic residue. In summer, dry dead stands of *H. spontaneum* are characterized by their fruit stuck vertically in the ground, the long stiff awns protruding upwards. This anchoring mechanism has apparently a selective advantage; seeds thus anchored are presumably protected from fire and from grazing and foraging animals. Later, this vertical position furnishes proper orientation for the germinating radicle. In fact, most diagnostic characters used by barley taxonomists to separate wild *H. spontaneum* from cultivated barleys (e.g. disarticulation of rachis; hairiness of rachis, rachilla and glumes; narrowness of fertile spikelet) are simply different manifestations of the biology of seed dispersal in this wild species. That this specialization is highly adaptive is further suggested by the presence of parallel dispersal biology and morphology in wild wheats (*Triticum dicoccoides, T. boeticum*) as well as several other members of the *Hordeae*.

In comparison, the dispersal triplet of *H. agriocrithon* is characterized by widely spread lateral spikelets. As a dispersal unit this triplet should be quite inefficient and its anchoring ability small, if any. This fact is most likely one of the main reasons why this form, even when apparently repeatedly produced in Israel, is unable to establish itself and is not found under truly wild conditions.

In conclusion, rather than being the wild ancestor of six-rowed barley, *H. agriocrithon* is most likely a hybrid derivative of it. Moreover, it is the author's view that the adaptive specialization found in the wild members of the barley group make it hard to visualize the survival of a wild six-rowed prototype. As originally proposed by de Candolle (1884) and by Körnicke (1885), *H. spontaneum* should be regarded as the likely wild progenitor of both two-rowed and six-rowed forms of cultivated barley. In domestication of wild barley man had mainly to alter the dispersal and germination biology. This done, selection for fertility of the lateral spikelets should have been relatively easy to achieve.

Literature Cited

Åberg, E. 1938. *Hordeum agriocrithon* nova sp., a wild six-rowed barley. Ann. Agric. Coll. Sweden, **6**: 159–212.

——. 1940. The taxonomy and phylogeny of *Hordeum* L. sect. Cerealia Ands. Symbolae Bot. Upsalienses, **4**(2): 1–156.

Anderson, E. 1953. Introgressive hybridization. Biol. Rev., **28**: 280–307.

Candolle, A. de. 1884. Origin of cultivated plants. 468 pp. Kegan Paul, Trench & Co., London.

Kamm, A. 1954. The discovery of wild six-rowed barley and wild *Hordeum intermedium* in Israel. Ann. Agric. Coll. Sweden, **21**: 287–320.

Körnicke, F. 1885. Die Arten und Varietäten des Getreides. Körnicke and Werner: Handbuch des Getreidebaues I. Berlin.

Schiemann, E. 1948. Weizen, Roggen, Gerste. 102 pp. Gustav Fischer, Jena.

Takahashi, R. 1955. The origin and evolution of cultivated barley. Adv. Genet., **7**: 227–266.

ORIGINS OF ANGIOSPERMOUS PLANTS[1]

VERNE GRANT

Rancho Santa Ana Botanic Garden, Claremont, California

"The origin and evolution of the angiosperms is one of the most provocative problems of modern biology, which has been attracting the attention of many a naturalist for a long time. Modern science, however, is still far from solving all the principal questions pertaining to the origin and the developmental history of the angiospermous plants. Therefore, in this book which we bring to the attention of the reader, he will find along with facts and generalizations definitely established by science, much that is hypothetical and much that reflects more than anything else the author's personal views." Thus writes Takhtajian in the Preface.

The principal conclusions reached by Takhtajian are as follows: (1) The angiosperms originated in the Jurassic or perhaps the Triassic period and persisted as subordinate elements of the flora until mid-Cretaceous time, when they rapidly rose to dominance. (2) The earliest angiosperms probably inhabited mountains in a subtropical zone (pp. 14, 22). (3) The important features leading to their evolutionary success were improvements in the conducting system (vessels), in the method of cross-pollination (flowers), and in the embryogeny (the angiospermous type of female gametophyte and endosperm). (4) The angiosperms probably have a common ancestry with the Bennettitales in some primitive group of seed ferns. (5) The most primitive characteristics still to be found in the angiosperms are scattered in various members of the Magnoliales. (6) The Fagaceae, Betulaceae, Casuarinaceae, Urticaceae, and Salicaceae are not primitive, but reduced and derived. (7) The monocotyledons probably arose from some herbaceous group of dicotyledons, perhaps the Nymphaeales, as adaptations for an aquatic or semi-aquatic life. (8) The Palmaceae, Pandanaceae and other arborescent monocotyledons are secondarily derived from herbaceous ancestors.

To Western botanists these conclusions come as no surprise. It is convenient, if not newsy, however, to have them summarized in one review article. The efforts of the translator, editor and publisher in making Takhtajian's essay available in English are justified to this extent.

What parts of Takhtajian's discussion represent "generalizations established by science" and what parts represent "the author's personal views" is difficult to tell, on account of an inadequate method of citing sources. Extensive passages contain no or only oblique references to the original literature from which they were drawn. The documentation is on the level of a teaching text rather than a scholarly work.

Chapter Six, for example, is devoted to a review of the morphological characteristics of the most primitive living dicotyledons, the woody Ranales. The facts presented here (which are absolutely basic for any discussion of primitiveness in the angiosperms) are taken almost entirely from a series of papers by I. W. Bailey and his collaborators. Several of the figures are taken from these same papers. But there is no mention of these sources anywhere in the chapter.

The bibliography in the Russian edition (but not in the translation) does list two articles by Bailey. In view of the much larger number of papers actually utilized as a basis for Chapter Six, and the omission of textual references to even these two, this effort at documentation must be judged incomplete by the standards generally accepted in scientific writing.

Similarly, the discussion of the relation of flower pollination to the early evolution of the angiosperms (pp. 15–20) contains very little material not to be found in five papers by myself in 1949 and 1950. My indebtedness to previous students of this classical question was acknowledged in these papers. Takhtajian's indebtedness to the more recent discussion of 1949–1950 is not so clearly stated, but is nevertheless evident from the internal structure of his presentation. Several whole sentences, in fact, have managed to survive very well in going from the original English to Russian and then back to English again.

Thus Takhtajian writes (p. 16), "More than 400 species of Mesozoic beetles are already known, which make up about 37 per cent of the insect fauna of that era." Grant wrote, "The Coleoptera were abundant throughout the Mesozoic, with over 400 species constituting 37 per cent of the fossil insect fauna of that era, according to Handlirsch (1925, p. 192) and Carpenter (1930, p. 26)." (Amer. Jour. Bot., **37**: 296, 1950.) The figure 37% was derived from an analysis of the data given by Handlirsch in his invaluable compendium of fossil insects, and not from any quotable statement of Handlirsch himself.

[1] Takhtajian, A. L. Origins of Angiospermous Plants. (Transl., Amer. Inst. Biol. Sci., Washington, 1958; original Russian edition, Soviet Sciences Press, Moscow, 1954.)

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To take another example, Takhtajian writes (p. 19), "The floral constancy is of a mutual benefit to both the flowers, which are better pollinated and waste less pollen and the insects, which are better fed." Grant wrote, "The instinct of flower constancy may thus have been preserved by natural selection, both for its advantage to the plant, which became better pollinated, and for its advantage to the insect, which became better fed." (Bot. Rev., **16**: 392, 1950.)

As my colleague, Dr. Sherwin Carlquist, points out to me, Chapter Eight on the origin of the monocotyledons is based largely on the ideas of Agnes Arber, whose connection with this discussion is not mentioned anywhere.

Any reader of "Origins of Angiospermous Plants" who was not acquainted with the original literature would gain the impression that large portions of this essay represent Takhtajian's original work and thinking. The "Origins of Angiospermous Plants," however, is not so much an original work as a compilation of the findings of other authors. These findings and ideas have been scattered widely in the literature; by bringing them together Takhtajian has performed a useful service. But the usefulness of his review paper is diminished by an inadequate citation of sources.

BOOKS RECEIVED

Notices will be given under this heading of books of evolutionary interest sent to the Editors. Appearance of a title in this section will not preclude a fuller review in a later issue of the journal.

Romer, Alfred S. 1959. The Vertebrate Story. VII + 440 pp., illus. $7.00. Chicago University Press. A complete revision of the well-known vertebrate zoology text, *Man and the Vertebrates,* by the author, the Director of the Museum of Comparative Zoology and Agassiz Professor of Zoology at Harvard University (former President of the Society for the Study of Evolution).

Cold Spring Harbor Symposium on Quantitative Biology, vol. XXIII. Exchange of Genetic Material: Mechanisms and Consequences. XVI + 433 pp., illus. $8.00. The Biological Laboratory, Cold Spring Harbor. A collection of 36 papers and record of discussions held at the annual symposium of the Long Island Biological Association.

Zirkle, Conway. 1959. Evolution, Marxian Biology and the Social Scene. 527 pp. $7.50. University of Pennsylvania Press. An analysis of the roots of Lysenkoism and of the impact of Marxist biology on evolutionary theory, literature and sociology.

Padoa, Emanuele. 1959. Storia della Vita sulla Terra. 338 pp. illus. 3500 Lire. Feltrinelli, Milan. An account of the evolution of plants and animals (not including man), forming part of a non-technical scientific series.

ERRATA

The following errors in the article by Masatako Kurabayashi (EVOLUTION, **12**: 286–310) should be corrected:

	Instead of	*Should read*
p. 287, table 1		
Chromosome number of *K. japonica*	3 X = 40	8 X = 40
p. 292, col. 1, line 13	*T. amabile*	*T. smallii*
p. 298, table 5		
N.T.C. value for *Nn* of Southern Hokkaido		
p. 301, table 6		
No. of *D* chromosomes under *Ak*	36	6